

THE RELATIONSHIPS OF THE ARCTOSTYLOPIDAE (MAMMALIA): NEW DATA AND INTERPRETATION

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ABSTRACT. The dental morphology of *Arctostylops steini*, hitherto known only from part of the lower cheek-tooth series, is described on the basis of a newly collected specimen including a nearly complete upper and lower dentition. All arctostylopoid materials from North America, principally from the Clarks Fork Basin, Wyoming, are apparently referable to this single species, which therefore ranges from the late Tiffanian through the Clarkforkian. Other arctostylopoid genera are restricted to the Asian Paleogene.

A previously described species of Asian *Palaeostylops* is placed in a new genus, *Gashatostylops*. The Arctostylopidae and its constituent subordinate taxa are diagnosed, and a hypothesis of relationships within the family is presented. By comparison with an ungulate morphotype as represented by *Protungulatum*, *Asiostylops spanios* is hypothesized to be the most primitive member of the family. *Bothriostylops notios* and *B. progressus* retain many primitive features but clearly bear some of the specializations seen in *Palaeostylops*, *Arctostylops*, and other advanced genera. Of these derived taxa, North American *Arctostylops* may be the sister taxon to the remaining genera, all of which are Asiatic in distribution. *Anatolostylops* and an as yet unnamed species are highly specialized sister taxa that may be most closely related to *Gashatostylops*.

Comparison of morphotypes for the Arctostylopidae and for southern Notoungulata suggests that derivation of one group from within the other as currently known, is unlikely. This comparison further indicates that most notoungulate similarities of arctostylopids were independently acquired and that the basis for an exclusive relationship of Arctostylopidae to Notoungulata as sister taxa is a single dental character. The ankles of arctostylopids and notoungulata are divergently specialized, and share no character not present in a eutherian morphotype. The Holarctic family Arctostylopidae is therefore removed from the Notoungulata. Relatives for the Arctostylopidae among Holarctic faunas remain unknown or unrecognized, although members of the group resemble several other enigmatic mammals from the Paleogene of Asia. Because it is a well-defined monophyletic unit without obvious close relationship to other mammalian groups, the Arctostylopidae is placed in its own order, Arctostylopida. Disassociation of the group from the Notoungulata removes the most compelling late Pa-

leocene or early Eocene link of Holarctic to Neotropical mammal faunas and suggests, in accordance with other evidence now available, that whatever inter-American connections of mammal faunas occurred must have been earlier in time. The geometry of hypothesized relationships among the Arctostylopidae and the fact that the group was most abundant and diverse in Asia suggest an Asian, rather than North or South American, origin for the family.

INTRODUCTION

Since the studies of Gaudry (1902, 1904, 1906, 1908) and Scott (1904), it has been widely accepted that South America's fauna is largely autochthonous, a result of that continent having been isolated by sea barriers from the rest of the world for most of the Tertiary. Endemism at high taxonomic levels is particularly conspicuous among the land mammals, which underwent their great diversification and radiations largely within the span of the Tertiary. It thus came as a great surprise when, in the first part of this century, apparent members of South America's largest and most characteristic group of hoofed mammals, the Notoungulata, were described from specimens recovered in Wyoming (Matthew, 1915) and Asia (Matthew and Granger, 1925; Matthew, Granger, and Simpson, 1929). Other possible close relatives among Holarctic and Nearctic mammal faunas had been and have continued to be suggested (Ameghino, 1906; Gingerich, 1985; McKenna, 1981). Nonetheless, none of the proposed relationships seemed so certain, based on characteristic synapomorphies, as in the case of these ungulates, for the Holarctic Arctostylopidae possess a strongly specialized dentition that resembles notoungulates alone among mammals. For this reason, the Arctostylopidae have figured prominently in discussions of the origin and early dispersal of South America's native land mammal fauna (McKenna, 1981; Simpson, 1951, 1978, 1980) and of zoogeography in general (Colbert, 1973; Darlington, 1957; Simpson, 1965). In addition, because of their presence in North America and Asia,

the Arctostylopidae have been integral to the development of correlations of early Tertiary strata (Dashzeveg, 1982; Gingerich and Rose, 1977; Matthew and Granger, 1925; Szalay and McKenna, 1971).

Arctostylops, represented by the type (and only) species, *A. steini*, was described by Matthew (1915), based on a partial lower jaw from the "lower Gray Bull beds, Clark Fork Basin, Wyoming." This locality is probably, but not certainly, Clarkforkian in age (Rose, 1981). Matthew referred the genus without question to the Notoungulata, hitherto known only from South America, placing it in the "Entelonychia," a mixed assemblage that then contained the most primitive of known notoungulates. Matthew believed *Arctostylops* to be early Eocene in age, which may well be the case, but is a matter of definition. Further materials of the species were not forthcoming for another 50 years, when a specimen was reported nearby from the Silver Coulee beds of the Polecat Bench Formation near Princeton Quarry. This locality is late Paleocene (late Tiffanian) in age (Jepsen and Woodburne, 1969). Intensive collecting by Gingerich, Rose, and associates in Clarkforkian beds of the Clarks Fork Basin has produced four additional specimens, consisting of dentulous lower jaw fragments and isolated teeth (Gingerich and Rose, 1977; Rose, 1981). The single report of *Arctostylops steini* from outside the Clarks Fork Basin is that of McKenna (1980), who recorded the species from beds of Clarkforkian age at Togwotee Pass, northwestern Wyoming.

However, related mammals had in the meantime been recovered from Asia. Paleontological work at Gashato in Mongolia by the American Museum of Natural History's Central Asiatic Expeditions led to the description of two species, *Palaeostylops iturus* Matthew and Granger, 1925 and "*P.*" *macrodon* Matthew, Granger, and Simpson, 1929. These species are probably latest Paleocene in age (Szalay and McKenna, 1971). More recent additions to the group have come from slightly

younger deposits at Naran Bulak, Mongolia (Gradziński et al., 1969), the Paleocene and Eocene (or possibly Oligocene) of China (Tang and Yan, 1976; Zhai, 1978; Zheng, 1979; Zheng and Huang, 1986), and the Paleocene of the USSR (Nesov, 1987), where seven additional described species, placed in six genera, bear witness to a modest radiation of Arctostylopidae in the early Tertiary of Asia.⁴ Tang and Yan (1976) described *Sinostylops*, including two species, from the late Paleocene of Anhui Province, China. *S. promissus* (from the Dou-mu Formation), the type species, is based on a mandibular ramus with eight teeth; *S. progressus* (collected in the Shuang-ta-si Group and later transferred to a new genus, *Bothriostylops*) from six jaw fragments. *Anatolostylops dubius* was described by Zhai (1978) from the putative early Eocene (but see below) Shisan-jian-fang Formation of the Turpan Basin, Xin-jiang Province, China. The species is known from a maxillary fragment with well-preserved M²⁻³. Two additional genera and species were published by Zheng (1979). *Asiostylops spanios*, from the late Paleocene Lan-ni-kong Member of the Chi-jiang Formation, Jiang-xi Province, China, is based on a skull and associated mandible preserving much of the dentition. Because of its primitiveness with respect to other members of the family, Zheng (1979) placed *Asiostylops* in its own monotypic subfamily. *Allostylops periconatus* Zheng, 1979, from the late Paleocene Wang-wu Member of the Chi-jiang Formation, Jiang-xi Province, is known from an incomplete rostral part of a skull with poorly preserved P² to M³. *Bothriostylops notios*, also from the Wang-wu Member of the Chi-jiang Formation, was described by Zheng and

Huang [1986]. These authors referred *Sinostylops progressus* to *Bothriostylops*. The most recent addition to the family is *Kazachostylops occidentalis*, described by Nesov (1987) from the late Paleocene Prestashkent Svita of Kazakhstan, USSR.

Since the initial descriptions of *Arctostylops* and *Palaeostylops* (Matthew, 1915; Matthew and Granger, 1925), students have realized that these Holarctic forms are, in some respects, more primitive than any known South American Notoungulata, while in other respects they are uniquely specialized. Their primitiveness is reflected by placement of the family Arctostylopidae in Simpson's archaic notoungulate suborder Notioprogonia (Simpson, 1934, 1945). However, the relationships of Holarctic to South American forms have never been considered in detail. For this reason, a variety of opinions exist as to the place of origin of notoungulates and their subsequent dispersal patterns, with authors variously favoring northern (Patterson, 1958) or, specifically, Asian (Matthew, 1928; Zheng, 1979); South American (Hoffstetter, 1970; Marshall, de Muizon, and Sigé, 1983; Simpson, 1951), and Central American (Gingerich and Rose, 1977) centers of origin.

Until recently, the data base for making such an assessment has been rather limited. The early Tertiary South American notoungulates have received monographic treatment (Simpson, 1945, 1967). The Holarctic radiation, the Arctostylopidae, was long represented only by the single lower dentition originally described for North American *Arctostylops steini* and by dentitions of two species referred to Asian *Palaeostylops*. Although some forms remain poorly known, Asian arctostyloid taxa described in recent years add substantially to knowledge of morphological diversity within the group, offering a dramatically improved basis for comparison with Notoungulata.

Herein we describe the dentition of *Arctostylops steini*, much of which has been hitherto unknown, based on a newly col-

⁴ An additional, undescribed genus and species has been reported from the late Paleocene Da-tang Member of the Nung-shan Formation, Guang-dong Province, China (Li and Ting, 1983). Dashzeveg (1982) recorded an undescribed species of "*Arctostylops*" from the Bumban Member of the Naran Bulak Formation, Mongolia, higher in the section than the local occurrence of *Palaeostylops iturus*.

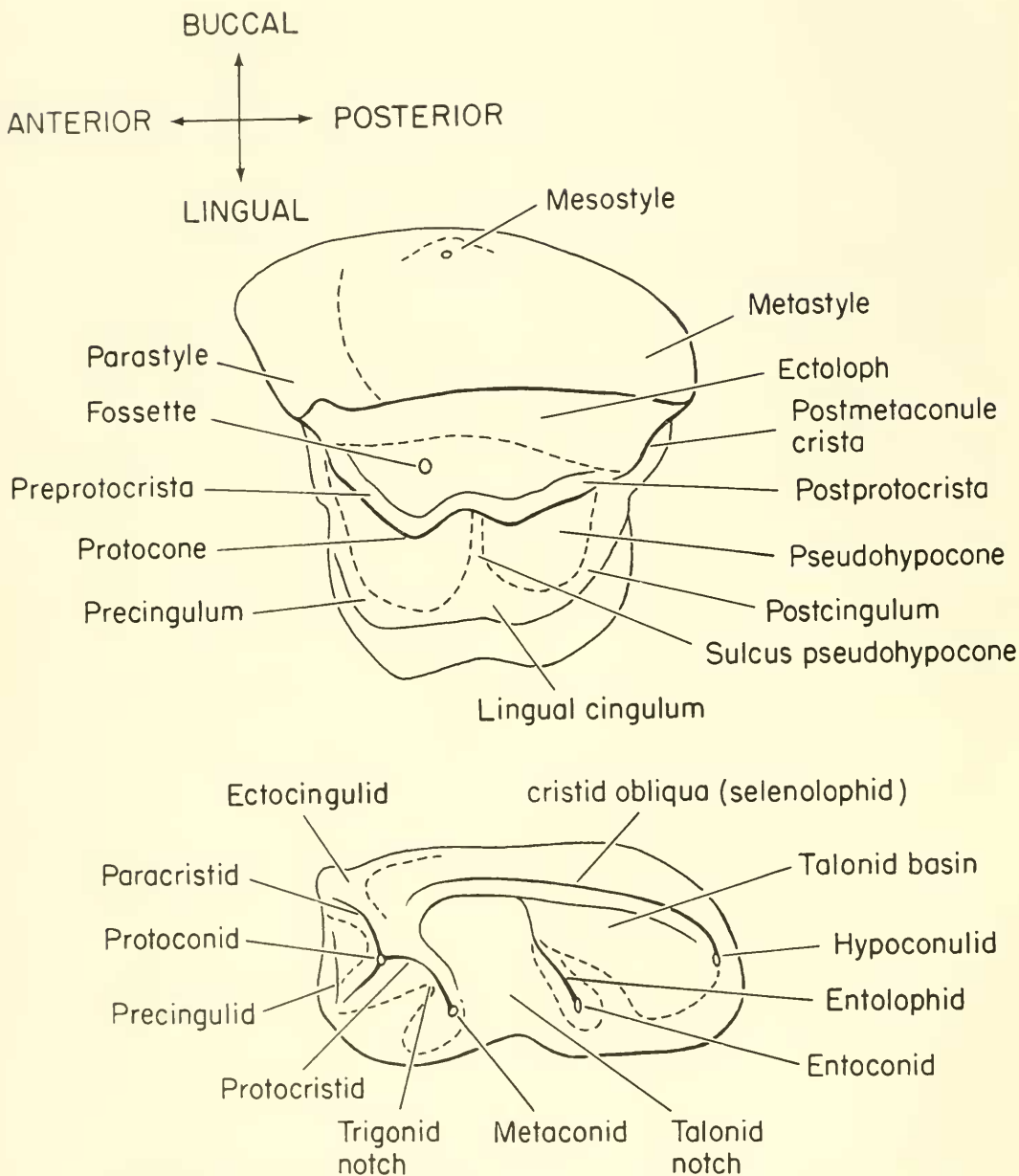


Figure 1. Dental terminology used in describing arctostyloid molars, based on *Palaeostylops iturus* (after Szalay, 1969).

lected and remarkably complete specimen from the late Tiffanian of Wyoming. This specimen forms the basis for a revised diagnosis of the genus and species and for a comparison with Asian Arctostylopidae and South American Notoungulata. Revised

diagnoses are presented for previously described taxa; we refer "*Palaeostylops*" *macrodon* to a new genus. Formal description of a hitherto unknown species of arctostyloid from the Yan-ma-tou Formation, Hunan Province, China, is currently

in progress; for comparative purposes, we briefly review some of its morphological features. Another new genus and species, from the Da-Tang Member of the Nungshan Formation, Guang-dong, is being described by others elsewhere.

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ABBREVIATIONS

AMNH, Department of Vertebrate Paleontology, American Museum of Natural History; IVPP, Institute of Vertebrate Pa-

leontology and Paleoanthropology, Beijing, People's Republic of China; MCZ, Museum of Comparative Zoology, Harvard University; UM, University of Michigan; YPM-PU, Yale Peabody Museum Princeton University Collection

Dental terminology is illustrated in Figure 1.

SYSTEMATIC PALEONTOLOGY

Order Arctostylopidae, new

Distribution. Extinct; presently known only from the Paleocene, Eocene, and possibly the Oligocene of Asia; late Paleocene and possibly early Eocene of North America.

Diagnosis. Small mammals with upper and lower dentitions forming an evenly graded series; canines poorly or not differentiated and without diastemata separating them from adjacent teeth. Posterior upper premolars somewhat molarized except in *Asiostylops*; P^4 , at least, with a metacone. Upper molars with well-developed centrocrista, becoming a salient, straight ectoloph in advanced genera, parastyle usually prominent. Pre- and postprotocristae of upper molars strong, conules lacking; upper molars primitively triangular but M^{1-2} becoming quadrate in advanced forms by the addition of a posterolingual cusp (pseudohypocone). Anterior lower premolars serially tricuspid, with strong shearing surfaces; lower molars primitively biselenodont, with paracristid lost and various accessory trigonid structures acquired in advanced taxa. Lower molar hypoconid indistinct, entoconid transversely expanded and, in advanced forms, developed into an anterobuccally oriented entolophid.

Family Arctostylopidae Schlosser, 1923, p. 614
(=Subfamily Arctostylopinæ Zheng, 1979, p. 391)

Type Genus. *Arctostylops* Matthew 1915, p. 429.

Other Included Genera. *Anatolostylops* Zhai, 1978, p. 109; *Asiostylops* Zheng

1979, p. 388; *Palaeostylops* Matthew and Granger, 1925, p. 2; *Sinostylops* Tang and Yan, 1976, p. 91; *Bothriostylops* Zheng and Huang, 1986, p. 121; *Kazachostylops* Nesov, 1987, p. 212; *Gashatostylops*, new; an unnamed genus; and, with some doubt, *Allostylops* Zheng, 1979, p. 391.

Distribution. Paleocene, Eocene, and possibly the Oligocene of Asia; late Paleocene and possibly early Eocene of North America.

Diagnosis. As for the order.

Zheng (1979) divided the Arctostylopidae into two subfamilies: the Arctostylopininae, which included "typical" genera; and the Asiostylopininae, containing only *Asiostylops* itself. While we are in agreement that this last-named genus is the most primitive of known forms, we choose not to recognize a higher taxon (subfamily) on that basis alone. Moreover, the description of species "intermediate" between *Asiostylops spanios* and advanced forms (see Zheng and Huang, 1986) largely occludes the morphological hiatus distinguishing the proposed subfamilies, so that they are not even clearly defined grades. Nesov (1987) distinguished two further arctostylopid subfamilies, Sinostylopininae and Kazachostylopininae. On the basis of evidence now in hand, we do not believe that such division of the group is warranted.

Arctostylops Matthew, 1915, p. 429

Type Species. *Arctostylops steini* Matthew, 1915, p. 429.

Included Species. The type only.

Distribution. Late Tiffanian to late Clarkforkian, and possibly Wasatchian, North America.

Diagnosis. Large arctostylopid differing from *Palaeostylops* and all other members of the family in having a salient lingual rib on the lower canine, a molarized P₄ with a low, recurved talonid loph that extends lingually at the posterior margin of the tooth, and a prominent anterolabial cingulum (ectocingulid). Distinct, where known, from primitive genera (*Asiostylops*, *Bothriostylops*) in having quadrate

upper molars with a sulcus separating two lingual cusps on M¹⁻². Upper molars differ further from those of *Asiostylops* in having a strongly developed ectoloph and in lacking a paracone fold. Lower molars differ from *Asiostylops*, *Kazachostylops*, and *Bothriostylops* in having paracristid reduced, prominent ectocingulid with shear surface descending from protoconid, cristid obliqua achieving a pronounced labial attachment to the trigonid, and entolophid stronger and more oblique. Metacones on P²⁻³ lacking or not so well-developed as in *Palaeostylops* and *Gashatostylops*; a lingual cingulum is present on P¹ and is more salient than in those genera. M¹⁻² more transverse, less quadrate in occlusal view; M² sulcus between protocone and pseudohypocone not so well-developed as in *Palaeostylops* or *Gashatostylops*. Metaconid of lower molars not forming a distinct column within the talonid basin as in those two genera. Pre- and postprotocristae of upper molars high and variably enclosing a very transient fossette, as occasionally seen in *Palaeostylops* and *Gashatostylops*, but not so strongly developed as in *Anatolestylops*.

Arctostylops steini Matthew, 1915

Figures 2, 8, 9

Arctostylops steini Matthew, 1915, p. 429; Jepsen and Woodburne, 1969, p. 546; Rose, 1981, p. 96⁵

Holotype. AMNH 16830, left mandibular ramus with P₃ to M₃.

Referred Material. MCZ 20004, associated mandible and anterior part of skull with nearly complete upper and lower dentitions; YPM-PU 20397, poorly pre-

⁵ The listing of this species as "*Palaeostylops steini*" by Thenius (1985, caption to Fig. 1, p. 151) deserves mention, although a text explanation is lacking and we are thus uncertain as to whether this is a *lapsus* or implied synonymy. The figure itself is diagrammatic but suggestive of *Palaeostylops iturus* rather than *A. steini* (for which well-preserved upper molars have not been previously reported otherwise). As indicated in the diagnoses, the species are clearly distinct; regardless, *Arctostylops* is the prior name.

A



B



Figure 2. Stereophotographs of upper (A) and lower (B) dentitions of *Arctostylops steini*, MCZ 20004

served, incomplete skull and mandible; UM 65024, left dentary fragment with worn M_2 , and right dentary fragment with P_3 ; UM 66707, right dentary fragment with M_1 and partial M_2 ; UM 68863, right M_2 ; UM 69280, right P_3 (UM specimens are cited from Rose, 1981, p. 96, and have not been studied by us); and AMNH 88141, trigonid of left M_1 .

Horizons and Localities. The type was collected in the "Lower Gray Bull beds, Clark Fork Basin, Wyoming" (Matthew, 1915, p. 429), of probable late Clarkforkian (Rose, 1981) or, possibly, Wasatchian (Jepsen and Woodburne, 1969) age. Referred specimens have been collected from the Willwood Formation at University of Michigan localities SC-19, 116, 188, and 203 in the *Plesiadapis cooki* and *Phenacodus-Ectocion* zones, Clarkforkian, Clarks Fork Basin, Wyoming (Rose, 1981, p. 96); in the "lower variegated sequence" (Love, 1947) of an unnamed formation, Clarkforkian, near Togwotee Pass, Wyoming (McKenna, 1980, p. 330); Silver Coulee beds, Polecat Bench Formation, *Plesiadapis simonsi* zone, Tiffanian (Jepsen and Woodburne, 1969, p. 546), Wyoming. The specimen described below, MCZ 20004, was collected by Charles Schaff and Mark Goodwin in 1977, approximately 5 m from the Princeton Quarry site (Jepsen, 1930). The specimen was excavated from a gray-green siltstone 2.5 m below the Princeton Quarry level. The locality (MCZ number I/77WYO; SE $\frac{1}{4}$ sec. 21, T56N, R100W) is about 24 km northwest of Powell, Park Co., Wyoming, on the west side of Polecat Bench.

Diagnosis. As for the genus.

DESCRIPTION

The upper and lower dentitions form evenly graded series, without diastemata or marked structural gaps between teeth. P^1 is not preserved in place in MCZ 20004. However, two isolated upper incisors, one of which has been lost, were found in association with the upper dentition and probably represent this tooth. The crown

is mitten-shaped, with a prominent distal heel. A cingulum, lacking on the labial side of the tooth, is well-defined on the lingual portion of the crown. I^2 is represented only by a fragmentary part of the crown. As with the preceding teeth, I^3 is single-rooted. The crests descending from the single cusp are sharp; a small heel is present. A weak labial cingulum is present; a lingual cingulum appears to have been well-developed, but breakage obscures most of this side of the tooth. The upper canine is similar to the incisors and, unlike those of *Palaeostylops* and *Gashatostylops*, which are subequal in size to adjacent teeth, is larger than I^3 and P^1 . The single root is round to oval in cross-section and is not well-differentiated from those of the adjacent teeth. The crown bears sharp mesial and distal crests, is labiolingually compressed, and is somewhat inclined posteriorly; the labial surface is convex and the lingual surface is slightly concave. The distal coronal crest bears a small, compressed cusp followed by a faint heel. The cingulum is well-defined both lingually and labially; the posterolabial part bears poorly defined cuspules. There are no diastemata adjacent to the canine.

P^1 is single-rooted and bears a single cusp. The tooth is labiolingually compressed, with a faint lingual bulge, and closely resembles the larger canine. The lingual cingulum is prominent. Salient crests descend from the anterior and posterior ends of the tooth to the single cusp. These evidently were important shearing structures, as a well-defined wear surface is developed on the lingual side of the tooth, obscuring any detail that may originally have been present. P^2 , also anteroposteriorly elongate, has two roots and is triangular in coronal view; the serial homologue of the protruding lingual cingulum on P^1 is here developed into a protocone. Labially, the ectoloph is supported by a single prominent cusp, the paracone, from which the loph descends anteriorly and posteriorly. The anterior surface is moderately worn, with the facet angled sharply with respect to the plane of occlusion. This facet is continuous with

TABLE 1. DENTAL MEASUREMENTS OF *ARCTOSTYLOPS STEINI*

	AMNH 16830	MCZ 20004	PU 20397	UM 65024*	UM 66707*	UM 67567*	UM 68268*
A. Lower dentition							
C ₁ L	—	—	—	—	—	—	—
W	—	—	—	—	—	—	—
P ₁ L	—	1.6	—	—	—	—	—
W	—	—	—	—	—	—	—
P ₂ L	—	3.0	—	—	—	—	—
W	—	1.8	—	—	—	—	—
P ₃ L	3.3	3.4	—	3.6	—	—	3.6
W	1.7	2.0	—	2.1	—	—	1.7
P ₄ L	3.7	3.8	—	—	—	—	—
W	1.8	2.0	—	—	—	—	—
M ₁ L	4.0	4.0	—	3.9	3.7	—	—
W	1.8	2.0	—	2.3	2.3	—	—
M ₂ L	4.2	4.7	—	—	—	3.4	—
W	2.1	2.3	—	—	—	2.2	—
M ₃ L	3.9	4.5	4.3	—	—	—	—
W	1.8	1.9	—	—	—	—	—
		MCZ 20004		PU 20397			
		L	W	L	W		
B. Upper dentition							
C ¹	3.1	2.0	—	—	—	—	—
P ¹	2.9	1.8	—	—	—	—	—
P ²	3.2	2.5	—	—	—	—	—
P ³	3.5	3.3	—	—	—	—	—
P ⁴	3.6	4.2	—	—	—	—	—
M ¹	3.7	4.9	—	—	—	—	—
M ²	4.5	5.6	—	3.7	4.1	—	—
M ³	4.0?	5.1	—	3.7	4.0	—	—

* From Rose (1981, p. 97).

another wear surface that extends from the region of the parastyle to the protocone, along the anterior portion of the lingual cingulum. A faint bulge anterior to the paracone suggests that in the unworn condition a parastyle was present. The part of the ectoloph distal to the paracone bears a strongly developed wear surface, also steeply angled with respect to the occlusal plane. P³ is larger than P², with a better developed protoconal region, more salient paracone fold on the labial surface of the ectoloph, and three roots, but is in most other respects similar to P². P¹ bears a well-developed, prominent protocone and is therefore considerably more transverse than P⁴. The ectoloph is folded at the paracone. The lingual surface of the ectoloph is considerably worn, but a parastyle and,

with less certainty, a metacone may be distinguished. A well-developed crest extends from the protocone to the parastyle. As with P³, wear on this crest is continuous with that on the anterolingual part of the ectoloph. The remnant of a small fossette persists in the trigon of the right P⁴. A well-developed cingulum extends from the parastyle around the base of the protocone and along the posterior border of the tooth. P⁴ is nearly the same length as M¹.

M¹⁻² are morphologically similar to each other, the principal difference being that M² is somewhat larger than M¹ (the difference in relative size is less in PU 20397). The ectoloph is anteroposteriorly straight, the only departure from this being the salient parastyle, which is developed as a column on the labial wall of the ectoloph

This ectoloph outer wall also has a postero-inferiorly developed bulge, probably corresponding to the base of a metacone or metastyle. The inner face of the ectoloph on each molar bears a very well-developed wear surface, oriented, as on the premolars, superolingually at a steep angle to the plane of jaw occlusion. A lingual sulcus separates the protocone from another cusp distal and somewhat appressed to it; this latter cusp we believe not to be a true cingulum hypocone, for reasons developed below. The crests linking protocone to parastyle (preprotocrista) and protocone to "pseudohypocone" (Gregory, 1920; Simpson, 1929) to the posterobuccal angle of the tooth (postprotocrista) maintained a primitive triangular arrangement with respect to the ectoloph and were evidently strongly developed, because a small remnant of a fossette enclosed by them persists on the left M^1 and right M^2 . These heavily worn crests descend⁶ buccally from the protocone to their junction with the descending wear surface of the ectoloph developed on the labial face of the trigon basin, so that the molars appear to be notched when viewed anteroposteriorly. M^3 , somewhat damaged on both sides of the specimen, is smaller and more triangular in outline than M^2 . An accessory crest, apparently lacking on M^{1-2} but perhaps not seen because of heavy wear on those teeth, sweeps posterolabially from the midpoint of the postprotocrista to the base of the metacone (or metastyle). A small accessory crest, the postmetaconule crista, is present on the left M^3 (the right M^3 is damaged). As with the more anterior molars, a distinct lingual cingulum is present and appears to be confluent around the base of the protocone.

The mandible is shallow and somewhat U-shaped at the symphysis. The symphysis

seems to have been unfused. Small mental foramina are located below the right P_4 and below left I_1 and I_2 , respectively.

I_1 is not preserved in MCZ 20004. I_2 is procumbent and spatulate, with a long straight root that is round in cross-section. An oblique ridge traverses the lingual surface of the crown. I_3 and the lower canine much resemble I_2 , differing in not being procumbent. The canine is thus incisiform, structurally undifferentiated, and not separated from adjacent teeth by diastemata. The crown of C_1 bears a well-developed lingual column; posterior to this, two cusps, separated by a notch, are present. P_1 is missing as a result of postmortem damage in MCZ 20004 and is represented only by a small remnant of one heel. The tooth was single-rooted. P_2 is a larger tooth and is double-rooted. It is buccolingually compressed and bears three principal cusps that are nearly in line with each other, the middle of which is the tallest. The anteriormost two cusps are separated by a distinct notch; the third cusp lies on the posterior slope of the middle cusp and has been reduced in this specimen by wear. Behind this the central crest slopes inferiorly before rising to a sharp heel at the distal margin of the tooth. A slight bulge is present on the inferolabial side of the tooth, but this is not distinctly formed into a cingulum. P_3 to M_3 are similar to those of the holotype, AMNH 16830, as figured by Matthew (1915). P_3 , like P_2 , is trenchant and is similar to that tooth except for being larger. P_4 is submolariform. The paraconid is lower than and directly mesial to the protoconid; the metaconid is lingually placed. The protoconid and the metaconid are subequal in size. The cristid obliqua attaches to the trigonid somewhat nearer to the metaconid than to the protoconid and extends superiorly to a level near the apices of these cusps. The talonid is formed by a simple, crescentic crest that terminates at the posterolingual angle of the tooth. A small anterolabial cingulum (ectocingulid) is present.

The lower molars are morphologically

⁶ For upper teeth, we follow convention in using the terms "ascend," "descend," "superior," "inferior," and so forth, in a sense relative to the way they are viewed, not with reference to orientation in life.

similar to each other. This series may differ slightly from that of the holotype, AMNH 16830, in that M_2 is more distinctly the largest of the three. The paraconid and its linking crest are altogether lacking, and the protoconid is near the anterolabial margin of the tooth. From this cusp a crest descends anterolabially, forming a distinct ridge (ectocingulid) at that corner of the tooth; the protoconid is also slightly expanded into an anterolingually developed ridge. The cristid obliqua has an extremely labial attachment to the trigonid; i.e., at the protoconid. From this point, at which it is nearly as high as the trigonid, it extends distally as a sharp, straight loph, before curving somewhat lingually to end at the hypoconulid. A hypoconid as such is lacking. The entoconid is transversely developed into a loph (entolophid), which extends anterolabially to join the principal talonid loph (cristid obliqua and posteristid) at about its mid-point. Measurements are given in Table 1.

Available materials of *Arctostylops* are inadequate to properly assess specific variability. All specimens in the hypodigm include teeth also represented in the type of *A. steini* (AMNH 16830) and are sufficiently similar to them in known morphological features to cause us to consider all specimens to belong to the same species. P_3 and M_1 are represented by four specimens each; M_2 and M_3 are known by three teeth each. Of these, M_2 shows a marked variability in length (Table 1). P_3 seems to vary considerably in proportion of length to width, but the significance of this cannot now be determined.

As thus recognized, the species *A. steini* is known from sediments of late Tiffanian (*Plesiadapis simonsi* zone) through Clarkforkian (*Phenacodus-Ectocion* zone) or possibly Wasatchian age. This is a wide stratigraphic range for mammalian species of that age; however, several other species, including the abundant phenacodontids *Phenacodus primaevus*, *P. vortmani* and *Ectocion osbornianus*, are believed to have similar ranges (Rose, 1981, pp. 22–23).

Palaeostylops Matthew and Granger, 1925, p. 2

Type Species. *Palaeostylops iturus* Matthew and Granger, 1925, p. 2

Included Species. The type only

Distribution. Late Paleocene to early Eocene (fide Li and Ting, 1983), Asia

Diagnosis. Dentally advanced arctostylopid generally similar to *Arctostylops* but differing in the lack of a heel on I_2 , lack of paracone folds on the ectoloph of P^{3-4} , lack of a lingual rib on C_1 , and in the lesser size differentiation of the upper canine from adjacent teeth. Molars lower-crowned than in *Anatolestylops*, upper molar fossette more rapidly lost by dental wear. Differs from *Gashatostylops macrodon*, the most closely similar form, in having a strong sulcus separating the lingual cusps of M^1 , three upper incisors, and an unconstricted snout, and in lacking cusps on upper molar lingual cingula and relative enlargement of the upper and lower second molars.

Both *Palaeostylops iturus* and *Gashatostylops macrodon* (herein separated from *Palaeostylops*) were described from the type Gashato Formation (Matthew and Granger 1925; Matthew, Granger, and Simpson, 1929). Both species, but especially *P. iturus*, are known from large samples of rather complete dental materials. Further remains of both species have been recovered in the Naran Bulak Formation by Soviet and Polish-Mongolian expeditions (Gradziński et al., 1969; Szalay and McKenna, 1971) to the Nemegt Valley, about 250 km WSW of Gashato; in the Nomogen Formation, near Nomogen, Nei Mongol, by Chinese workers (Chow et al., 1977; Chow and Qi, 1978); and in the Bayan Ulan Formation, Nei Mongol (Qi, 1979). Individuals of these species represented by far the most abundant members of the Gashato and Nomogen faunas, a curious fact considering the scarcity of their close relative, *Arctostylops*, in nearly contemporaneous North American faunas.

Varied opinions exist as to the status of

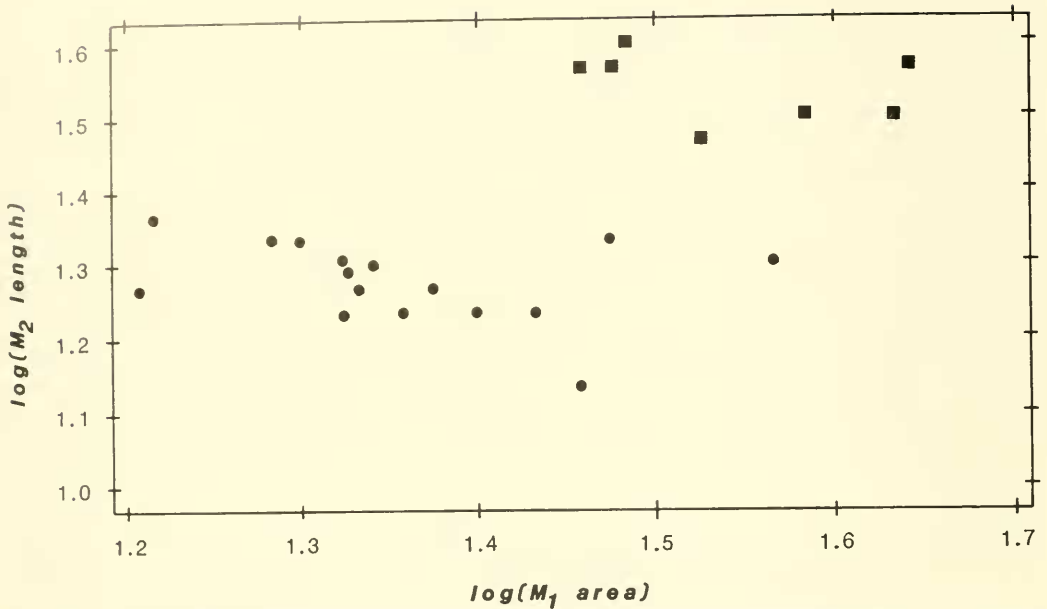


Figure 3. Plot of log-transformed M_1 area vs. M_2 length for *Palaeostylops iturus* (dots) and *Gashatostylops macrodon* (squares).

the genus *Palaeostylops*, its contained species, and the relationships of those species to *Arctostylops steini*. Simpson (1936a) indicated that the species *P. iturus* and "*P.*" *macrodon* might be considered as closely allied but distinct genera; Dashzeveg (1982) referred both to the North American genus *Arctostylops*. The superficially close similarity of the Asian species (except for size) and the fact that they always co-occur suggested to us, at the outset of this study, the possibility that a single, sexually dimorphic, species was represented. Detailed qualitative and quantitative comparisons, presented below, together with previously unknown morphology provided by a new specimen, uphold Simpson's view. To explore the differences between these superficially similar species, we examined available (AMNH) samples of arctostyloid dentitions from the Gashato and Nomogen localities and performed univariate and multivariate analyses on tooth dimension (length, width) data, using the Systat microcomputer software package.

Matthew, Granger, and Simpson (1929)

distinguished "*P.*" *macrodon* from *P. iturus* by its larger size and its proportionately larger second upper and lower molars. Comparison of type and referred materials reveal several other consistent morphological differences, summarized in the diagnoses and description given below. The most obvious difference in specimens assigned to the two species, other than absolute size, is the aforementioned disproportionately large upper and lower second molars of "*P.*" *macrodon* (Table 2). Length measurements of these teeth do not even overlap in range, which would be expected if the difference were due to sexual dimorphism. In most mammals (Gingerich, 1974), M_1 is the least variable lower molar; in *Palaeostylops iturus*, the species for which samples are most nearly adequate, variability is comparable between M_1 and M_3 (Table 2). Because M_1 is represented by larger samples in both species, this tooth was chosen as a basis for comparison of second molar proportionate size. A plot (Fig. 3) of log-transformed M_1 area (length \times width) against M_2 length indicates that the difference in relative length of the sec-

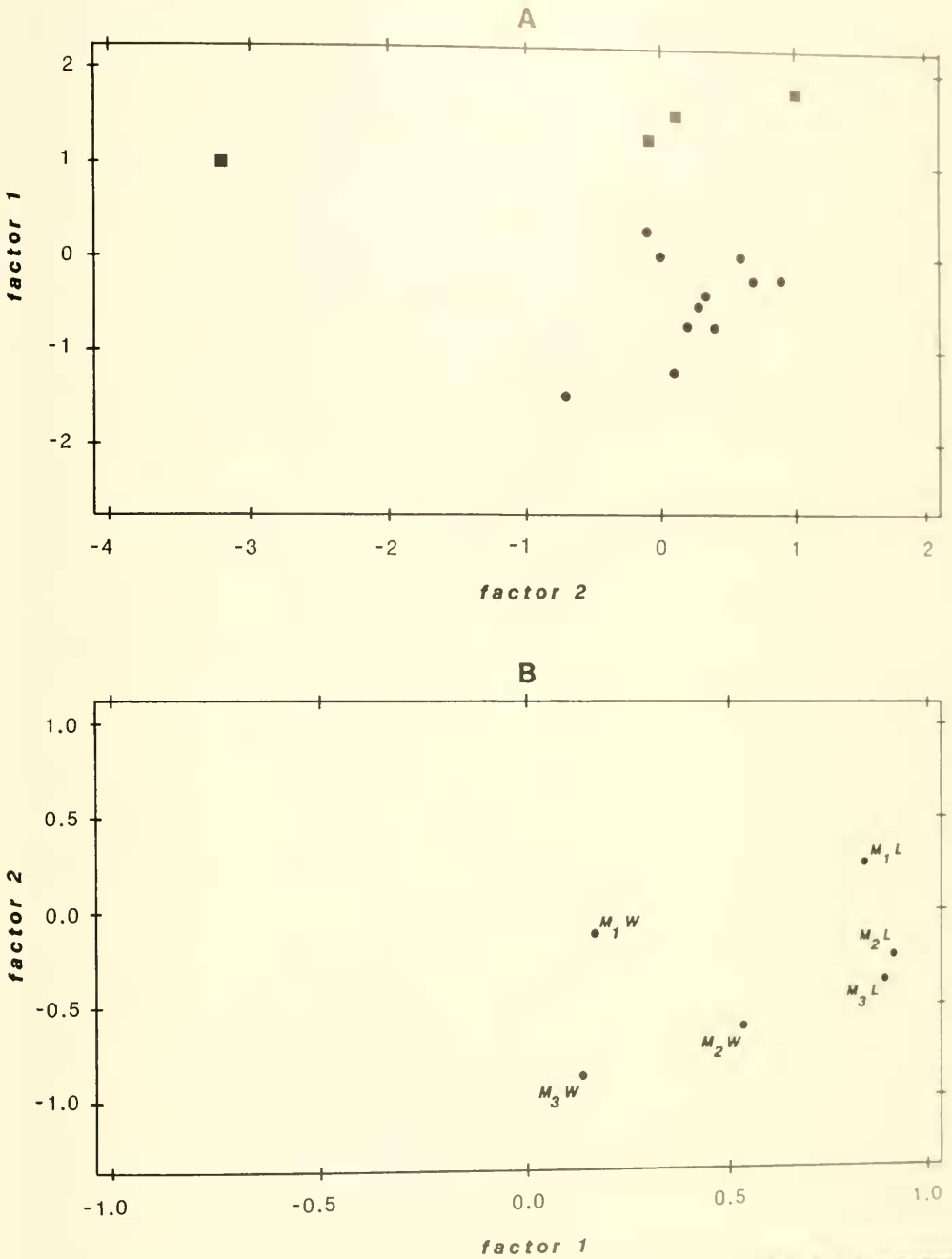


Figure 4. PCA loading plots for six lower molar variables of *Palaeostylops* and *Gashatostylops*. A, individual specimen loadings on first two axes (dots = *P. iturus*; squares = *G. macrodon*); B, loadings for the six variables on the first two axes.

TABLE 2. MEASUREMENTS AND SUMMARY STATISTICS OF PALAEOSTYLOPS AND GASHATOSTYLOPS (MM; P = *P. ITURUS*, G = *G. MACRODON*).

A. Upper cheek teeth										
	P ³ L		P ³ W		P ⁴ L		P ⁴ W		M ¹ L	
	P	G	P	G	P	G	P	G	P	G
N	2	2	2	2	4	2	3	2	5	5
Minimum	1.880	2.140	1.690	1.850	1.410	2.070	2.210	2.290	2.260	2.670
Maximum	1.990	2.170	1.880	2.000	2.090	2.120	2.320	2.530	2.700	3.220
Mean	1.935	2.155	1.785	1.925	1.812	2.095	2.273	2.410	2.532	2.936
SD	0.078	0.021	0.134	0.106	0.304	0.035	0.057	0.170	0.170	0.210
	M ¹ W		M ² L		M ² W		M ³ L		M ³ W	
	P	G	P	G	P	G	P	G	P	G
N	5	5	5	5	4	5	4	3	3	3
Minimum	2.340	2.790	2.670	4.320	3.170	3.630	2.030	1.940	2.570	3.020
Maximum	2.960	3.340	3.560	5.190	3.530	4.100	2.340	2.530	3.060	3.100
Mean	2.772	3.026	3.138	4.788	3.398	3.874	2.135	2.323	2.810	3.063
SD	0.250	0.209	0.328	0.321	0.161	0.177	0.139	0.332	0.245	0.040
B. Lower cheek teeth										
	P ₃ L		P ₃ W		P ₄ L		P ₄ W		M ₁ L	
	P	G	P	G	P	G	P	G	P	G
N	7	3	7	3	10	4	9	3	16	7
Minimum	1.760	2.090	0.980	1.230	1.960	2.500	1.040	1.300	2.440	2.890
Maximum	2.310	2.370	1.220	1.280	2.500	2.700	1.280	1.440	2.950	3.220
Mean	2.011	2.240	1.164	1.253	2.303	2.612	1.170	1.393	2.737	3.064
SD	0.208	0.141	0.086	0.025	0.153	0.084	0.081	0.081	0.120	0.141
C Var	10.3	—	7.3	—	6.6	—	6.9	—	4.4	—
	M ₁ W		M ₂ L		M ₂ W		M ₃ L		M ₃ W	
	P	G	P	G	P	G	P	G	P	G
N	16	7	16	12	16	12	11	4	11	4
Minimum	1.270	1.420	3.060	4.150	1.510	1.750	2.370	3.090	1.330	1.330
Maximum	1.630	1.610	3.850	4.890	2.010	2.550	3.030	3.320	1.520	1.800
Mean	1.425	1.533	3.537	4.592	1.744	2.063	2.694	3.185	1.407	1.505
SD	0.140	0.077	0.194	0.248	0.145	0.248	0.172	0.097	0.060	0.205
C Var	7.3	—	5.5	—	8.3	—	6.4	—	4.3	—

ond molar between the two morphs is not a factor of scaling, i.e., an allometric effect attributable to the fact that "*P.*" *macrodon* is larger than *P. iturus*. Were this the case, all specimens would have fallen along the same line; in the present situation, two lines, with different Y-intercepts, are apparent. To evaluate the significance of differences in measurement means, independent T-tests were performed on the lower cheek-tooth data. For most variables, means of samples assigned to the two species were significantly different at the .05 level (Table 3): probability of identical means was highest for P₃L, P₃W, M₁W, and M₃W and lowest for M₁L, M₂L, M₃L, and

M₂W. Principal components analysis, which does not require prior taxonomic sorting, was performed on various combinations of both untransformed and log-transformed lower molar data (the correlation matrix with listwise deletion of missing data and varimax rotation were employed). These analyses consistently separated the specimens into two groups (corresponding to the two species) along the first axis (presumably attributable to size) that, for the untransformed and unrotated lower molar data, accounted for about 61% of the total variance. Factor loading plots (Fig. 4) indicate that the source of this separation is the three length

variables (M_1L , M_2L , M_3L), which have very high loadings along the first axis; a result consistent with the univariate analysis.

Thus, on a statistical basis, the differences between *P. iturus* and "*P.*" *macrodon* are significant and are not attributable to size alone. In addition, dental and cranial features indicate greater structural differences between the species than has hitherto been appreciated. We consider these differences to be worthy of generic separation.

Palaeostylops iturus Matthew and Granger, 1925, p. 2

Arctostylops iturus Dashzeveg and Russell, 1988, p. 131

Figures 7, 8

Holotype. AMNH 20414, right mandibular ramus with broken I_{1-2} and with I_3 to M_3 complete.

Referred Specimens. The type, and the following AMNH specimens, consisting of dentulous upper and lower jaws or portions thereof: 20415, 20417, 22143, 101967, 101968 (uppers); 20429, 21723, 101983, 101985; and AMNH 109522 A–J, casts of 10 uncatalogued lower jaw specimens in the IVPP. The AMNH specimens are from Gashato; the IVPP specimens were collected at Nomogen. Additional materials referable to the species are housed at the Polish Academy of Sciences, Warsaw, and at the Paleontological Institute, Moscow. These specimens are not listed here because we were not able to compare them directly with the fossils listed above.

Horizon and Localities. Late Paleocene; Gashato, Bayan Ulan, Naran Bulak, and Nomogen formations, Nei Mongol.

Diagnosis. As for the genus.

Gashatostylops, new genus

Type Species. *Palaeostylops macrodon* Matthew, Granger, and Simpson, 1929, p. 11.

Etymology. Gashato-, for the original locality of the type species; -stylops (Gr.), pillarlike, a commonly-used suffix for arc-

TABLE 3. HOMOGENEITY OF GROUP MEANS FOR LOWER CHEEK TOOTH MEASUREMENTS OF *PALAEOSTYLOPS ITURUS* AND *GASHATOSTYLOPS MACRODON*.

Variable	T Statistic	Prob. identical means
P_3 length	1.714	0.125
P_3 width	1.708	0.126
P_4 length	3.768	0.005
P_4 width	4.140	0.002
M_1 length	5.725	0.000
M_1 width	2.456	0.023
M_2 length	12.650	0.000
M_2 width	4.267	0.000
M_3 length	5.320	0.000
M_3 width	1.501	0.157

tostylopid and primitive notoungulate genera.

Distribution. Late Paleocene to early Eocene (*vide* Li and Ting, 1983), Asia.

Diagnosis. Advanced arctostylopid differing from *Palaeostylops*, the most closely similar genus, in having relatively enlarged upper and lower second molars; in having cuspules, variable in number and development, on the lingual cingula of upper molars; in the weakness or absence of a sulcus separating the lingual cusps of M^1 ; in the presence of two rather than three upper incisors; and in having a laterally constricted snout, with the dental arcade multiply curved. Differs from *Anatolostylops*, to which it may be closely related, in having lower-crowned cheek-teeth and in having upper molars with accessory cusps and plications on the lateral walls of the ectolophus.

Gashatostylops macrodon (Matthew, Granger, and Simpson, 1929)

Palaeostylops macrodon Matthew, Granger, and Simpson, 1929, p. 11

Figures 5–9

Holotype. AMNH 21725, left mandibular ramus with P_3 – M_2 .

Referred Specimens. The type, an uncatalogued IVPP specimen (casts, AMNH 109521) consisting of the left rostral part of a skull with roots of two right and left incisors, left C– M^1 , and part of the left mandible with M_3 , plus an astragalus, col-

lected by McKenna; AMNH 21742, two isolated calcanea; AMNH 21726, isolated right astragalus; and the following AMNH specimens consisting of dentulous upper and lower jaw fragments: 22142, 101967, 101979, 101977, 101963 (maxillary); 101980, 101987, 101984, 101982, 101981, 20416, 21740, 21741, 21723, and 21716 (mandibular). The AMNH specimens were collected at Gashato, the IVPP specimen is from Bayan Ulan. As with *Palaeostylops iturus*, additional specimens (not listed here) are in the collections of the Polish Academy of Sciences, Warsaw, and the Paleontological Institute, Moscow.

Horizon and Localities. Late Paleocene; Gashato, Bayan Ulan, Naran Bulak, and Nomogen formations, Nei Mongol.

Diagnosis. As for the genus.

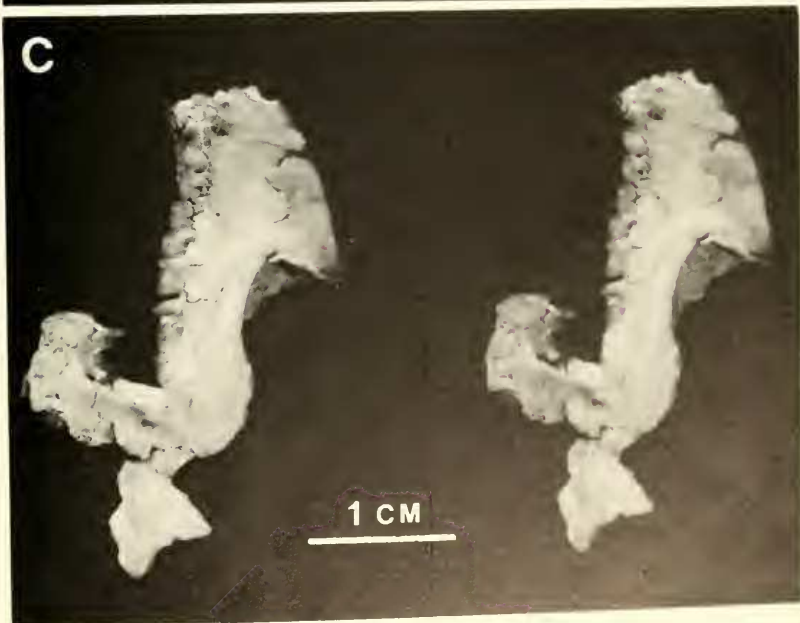
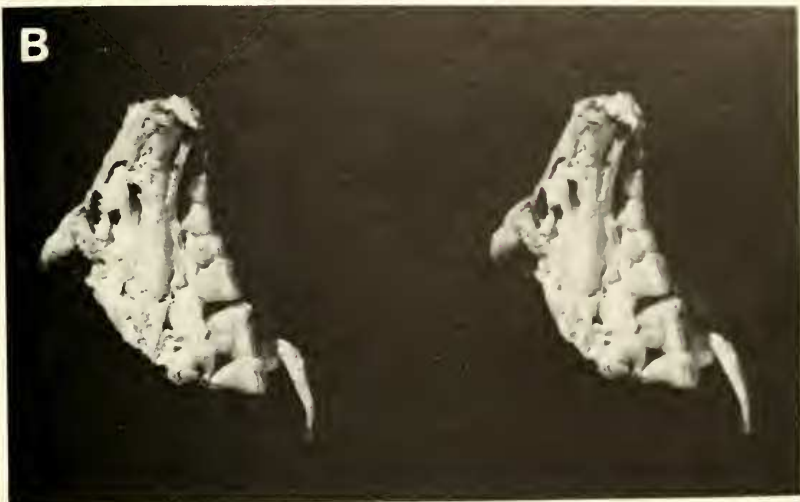
Although a diagnosis appeared in the original publication (Matthew, Granger, and Simpson, 1929), the morphology of this species has never been described. Important details are provided by the specimen represented by AMNH 109521 from Bayan Ulan, which preserves the left side of the rostrum, including the orbit and zygomatic root, left C-M₃, and the roots of the incisors on both sides. In addition, further preparation of the original IVPP specimen by one of us (Schaff) revealed the presence of part of the left mandible, including M₃ and the condyle, and a right astragalus lodged within the broken cranial cavity. These are presumed to be associated with the skull fragment itself. All teeth are in full eruption but wear is light, indicating that the animal was a young adult. The specimen is more or less split sagittally, except that both premaxillae are preserved. The palate, nasal, and frontal regions are crushed, so that the corresponding bones are somewhat fragmented. Comparison with the dentition preserved in original paratypes of the species (AMNH 22144, left P¹-M²; 22142, right broken M¹

and complete M²⁻³) and other referred materials from the type locality leave no doubt as to reference of this specimen to *Gashatostylops macrodon*.

As preserved in AMNH 109521, the snout is short and constricted, flaring broadly at the root of the zygomatic arch, so that in palatal aspect the tooth row assumes a double curvature. The form of the dental arcade thus contrasts with that seen in *Palaeostylops iturus*, which curves gently from front to back. In palatal view, the posterior margin of the maxilla forms a curved process that almost completely encloses a small foramen lingual to the junction of M² and M³. This foramen in all probability housed the minor palatine branch of the maxillary artery, as it does in many living mammals and in certain notoungulates, such as *Notopithecus* (see Simpson, 1967, fig. 23). The infraorbital foramen, located above the junction of P³ and P⁴ about halfway between the base of those teeth and the anteroinferior margin of the orbit, is small. The root of the zygomatic arch arises at the base of M². It is massive and dorsoventrally expanded, flaring to an inferior prominence at the squamosal suture, suggesting relatively powerful development of the masseteric musculature. The nasals are long and narrow, flaring posteriorly, with the median processes of the frontals deeply projecting between them. Small, isolated foramina are present in each nasal. The premaxillary-maxillary suture is located in the most anterior quarter of the snout, just posterior to I². The maxilla is extensive, incorporating three-quarters of the snout region, and extends to the base of the orbit. The maxillary-jugal suture is oblique and runs above the base of M³.

Although upper incisors are not preserved in the specimen represented by AMNH 109521, roots preserved in the premaxillae clearly indicate that only two were

Figure 5 Stereoscopic views of rostrum of *Gashatostylops macrodon* and associated partial left mandible (uncatalogued IVPP specimen, cast. A, dorsal; B, ventral; C, left lateral views).



present on each side, in contrast to the three known for *Palaeostylops iturus* and *Arctostylops steini*. The roots of both incisors are subround and approximately equal in size. The base of the upper canine is larger than the roots of the incisors, approximating the base of P¹ in size. Whether or not this reflects a notable difference in size between canine and lateral incisor crowns cannot be determined; however, root development is comparable in *Palaeostylops iturus*, whose anterior teeth nonetheless form an evenly graded series (cf. Matthew, Granger, and Simpson, 1929, p. 12). P¹ is single-rooted. Its crown, generally similar to those of corresponding teeth in *Palaeostylops* and *Arctostylops*, is buccolingually compressed and bears a sharp mesiodistal crest, which ascends medially to the apex of the single cusp. A faint lingual cingulum, not developed into a heel as in *Palaeostylops*, is present. P² is double-rooted. It is larger than P¹ and structurally similar to it, except that a protocone, smaller than that of *Arctostylops* and equal to that of *Palaeostylops*, is developed lingually. Well-defined crests descend from this cusp to the anterior and posterior margins of the tooth. The lingual surface of the coronal crest, or ectoloph, is steep and bears well-marked wear facets, as seen in succeeding teeth. P³⁻⁴ are successively larger and more molariform, with more fully developed protocones. As in *Palaeostylops iturus* but in contrast to *Arctostylops steini*, P⁴ is noticeably smaller than M¹. The molars bear sharp, straight ectolophs with well-developed parastyles. On M¹, the lingual sulcus posterior to the protocone is faint, unlike the condition seen in *Palaeostylops*. Lingual cingula are well-developed on all upper molars; cusps, variable in development, are present on M¹⁻². M¹ in the specimen represented by AMNH 109521 bears two such cusps, one lingual to the protocone and another, larger, posterolingual to that cusp and in a hypoconal position. M² is much larger than preceding or succeeding teeth and bears three cusps on the lingual cingulum. Posterior to the

protocone the lingual sulcus is strong, so that the tooth is bilobed. A prominent accessory cusp lies in a median position at the base of the ectoloph, posterior to the parastyle. M³ is generally similar to those of *Arctostylops steini* and *Palaeostylops iturus*, except that the lingual cingulum is complete and bears an eminence directly lingual to the protocone.

A nearly complete lower dentition is represented in AMNH 21741 from Gashato, a left dentary with I₁₋₃, C, P₁₋₄, and M₁₋₃; the last molar bears a moderately damaged talonid. The horizontal ramus is shallow, with a nearly horizontal symphysis that appears to have been unfused. Small foramina are located below P₁ and P₄. The three incisors are similar to those of *Palaeostylops iturus*. I₁ is spatulate with a rounded point and a median vertical ridge, the crown being less compressed than in *Arctostylops steini*. I₂ is larger and more laterally compressed than I₁, with the anterior part of the crown more expanded and the median vertical ridge better developed. I₃ is similar in size and morphology to I₂, except for the presence of an incipient posterior lobe on the median ridge. The canine is subequal in size to I₃ and somewhat larger than P₁; no diastemata separate it from those teeth. The crown of the canine is tricuspid and compressed; lingual crests are associated with each cusp. In these respects it generally resembles *Palaeostylops iturus* rather than *Arctostylops steini*.

The single-rooted P₁ is morphologically similar to the canine, although the three coronal cusps are somewhat more distinct. P₂ is double-rooted and significantly larger than P₁, with the tricuspid pattern clearly defined. P₃ is similar to but larger than P₂, with the protoconid being the tallest cusp. P₄ is submolariform, with a serially tricuspid trigonid and a small, crested heel. The paraconid and metaconid are equal in size, and the protoconid is the tallest cusp. The cristid obliqua attaches somewhat labial to the metaconid. There is no ectocingulid present on any of the lower premolars.



Figure 6. Stereophotographs of left mandible of *Gashatostylops macrodon*, AMNH 21741

The most notable feature of the lower molars is the extremely salient, blade-like, labially-placed cristid obliqua. The molars are morphologically similar to each other, with M_2 appearing to be disproportionately larger than preceding and succeeding teeth. The entoconid is expanded into an obliquely-oriented entolophid that contacts the cristid obliqua in about the middle of the talonid. On all three molars, the ectocingulid is developed as a distinct anterolingual ridge at the junction of protoconid and cristid obliqua. The protoconid is the tallest cusp except on M_2 , in which the hypoconulid is larger.

No directly associated, articulated postcranial elements are yet known for any of the Arctostylopidae, but proximal ankle bones may now be referred to *Palaeostylops iturus* and *Gashatostylops macrodon* with little doubt. These species are by a considerable margin the most abundant taxa known from Gashato. Isolated astragali and calcanea, of appropriate size for *P. iturus* and *G. macrodon*, occur there in the same relative abundances as dental remains of these species. Furthermore, an astragalus was found lodged within the cranial cavity of a specimen from Bayan Ulan referred to *G. macrodon* (see below). This astragalus, for which association is

reasonably inferred, resembles to the point of identity the isolated specimens from Gashato believed on the basis of size and relative abundance to belong to *Gashatostylops macrodon*. In known respects, the ankle of *Palaeostylops iturus* is similar to that of *G. macrodon*, and it is therefore not described separately. Descriptive terminology follows that of Cifelli (1983b). Relative terms in the description are based on comparison with ankle bones referred to *Protungulatum* and similar taxa, which are assumed to approximate a eutherian morphotype (Szalay and Decker, 1974; Szalay, 1977).

As represented by AMNH 21726, a right astragalus from Gashato, the astragalar body is mediolaterally compressed, with nearly vertical sides; there is little or no development of a fibular shelf on the lateral side. The body is more or less cylindrical, with the tibial trochlea marked by a median groove and well-defined, raised borders. An astragalar foramen is apparently lacking; a pit is present on the tibial trochlea of AMNH 21726, but appears to have been caused by diagenetic corrosion of the fossil (as on the other side of the same specimen; such pitting is common on fossils from Gashato). The neck is of moderate length but is notably constricted, so

that the head is clearly demarcated. The head itself is subround with, however, the navicular facet developed as a flattened band that does not extend onto its sides. The navicular facet extends far superiorly, onto the dorsal side of the bone, and is developed so that movement between astragalus and navicular would have been subparallel rather than highly oblique to that between astragalus and tibia. There is no observable separate facet for the cuboid. The tarsus might thus tentatively be regarded as "serial" (see discussion by Osborn, 1889), although this cannot be definitively ascertained until a well-preserved, articulated foot is discovered. The sustentacular facet is unremarkable, except that it is somewhat larger and better developed distally than it is in *Protungulatum*. The ectal facet is very steeply inclined, and the interarticular sulcus separating the two facets is deep.

The calcaneus, as represented by AMNH 21742 (complete left calcaneus and right calcaneus lacking the tuber, almost certainly not from the same individual), is notable in having a short neck (that part anterior to the astragalocalcaneal facets) relative to the tuber. The ectal prominence is dominated by a very strongly developed fibular facet, which forms a broad, antero-posteriorly oriented, semicylindrical surface. Medial to this lies the ectal facet, which is strongly inclined with respect to the fibular facet. The sustentaculum is unusual in lying at or near the distal end of the bone; a prominent "beak" is developed on the superior distomedial corner of the bone. The cuboid facet is developed at a moderate angle with respect to the long axis of the calcaneus. Comparisons to other taxa are deferred until the discussion.

Sinostylops Tang and Yan, 1976, p. 91

Type Species. *Sinostylops promissus* Tang and Yan, 1976, p. 92.

Included Species. The type only.

Distribution. Late Paleocene (*vide* Li and Ting, 1983), Asia.

Diagnosis. Primitive arctostyloids differing from *Asiostylops* in having higher-crowned molars and a metaconid on P_{33} . Distinct from advanced genera such as *Arctostylops* in retaining a paracristid on the lower molars. Similar to *Bothriostylops* in having the cristid obliqua attaching to the trigonid of lower molars in a lingual position, but differs from that genus in having higher-crowned molars and a more slender, elongate P_3 .

Sinostylops promissus Tang and Yan, 1976, p. 92

Holotype. IVPP V4263, right mandibular ramus with eight partial or complete teeth.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 71017, Dou-mu Formation, Anhui Province, People's Republic of China; late Paleocene.

Diagnosis. As for the genus.

With the removal of referred species "*Sinostylops*" *progressus* to *Bothriostylops*, the concept and affinities of *Sinostylops* become problematic. The identities of the eight teeth in the holotype and only specimen of *Sinostylops promissus* are open to doubt. Because the third from the last tooth is remarkably low-crowned and long, unlike either preceding or succeeding teeth, we believe it to be deciduous. The penultimate tooth, although much smaller than the ultimate, is morphologically similar to it; both are badly damaged but apparently were bicrescentic, which is not the case for the more anterior teeth. We therefore believe the teeth in this specimen to be I_3 - P_3 , dP_4 , and M_{1-2} , although other interpretations are possible. Available materials of *Sinostylops promissus* and *Bothriostylops progressus* suggest further differences between the species beyond those listed in the diagnoses, but because of the uncertain identities of the teeth in IVPP 4263 and because of postmortem damage to that specimen, we are unable to evaluate the significance of these differences.

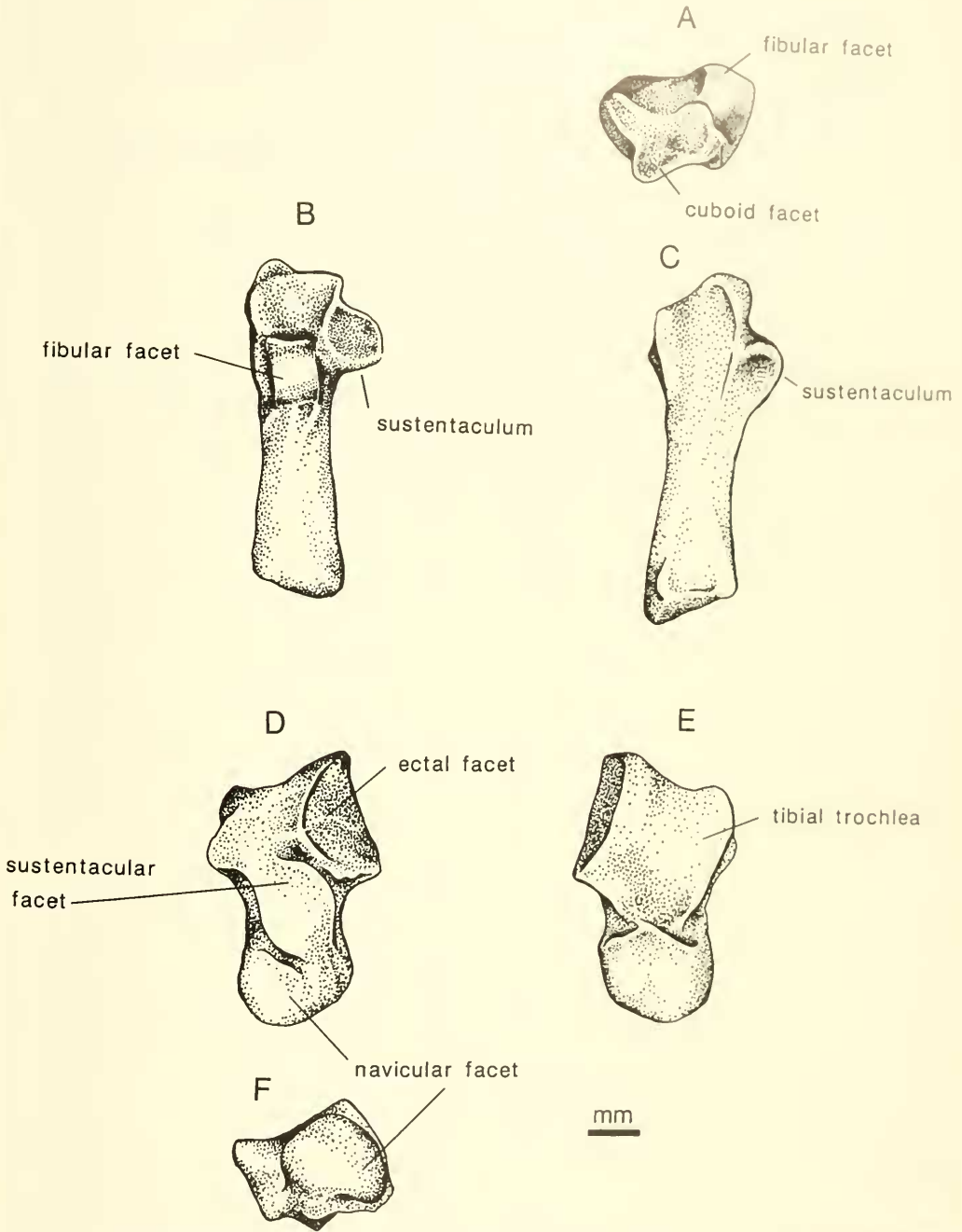


Figure 7. Right astragalus (unnumbered IVPP specimen associated with rostrum of skull, a cast of which is numbered AMNH 109521) and left calcaneus (AMNH 21742) of *Gashatostylops macrodon*. A, B, C: calcaneus in distal, dorsal, and plantar views respectively; D, E, F: astragalus in plantar, dorsal, and distal views, respectively.

Bothriostylops Zheng and Huang, 1986, p. 121

Type Species. *Bothriostylops notios* Zheng and Huang, 1986, p. 122.

Referred Species. The type, and *Bothriostylops progressus* (Tang and Yan, 1976, p. 92).

Distribution. Late Paleocene, Asia.

Diagnosis. Primitive arctostyloids with brachydont teeth, differing from *Asiostylops*, which they generally resemble, in having a crescentic P_4 talonid; and from all known genera in having M_3 with an elongate talonid, the hypoconulid forming a distinct lobe.

A number of other characters were listed in the diagnosis and description of the genus (Zheng and Huang, 1986). Of these, the presence of a deep median labial groove and convex labial wall on lower molars were cited as important similarities to *Asiostylops*. We see no distinction of arctostyloid genera on this basis but, lacking access to the original specimens (especially the type of *Bothriostylops notios*), we defer to Zheng and Huang (1986). Nonetheless, we observe that a deep median external groove is present on lower molars of *Sinostylops promissus*. Even on the basis of the single, enigmatic specimen available, it is clear that this latter species is rather divergent and not obviously congeneric with other known taxa.

Bothriostylops notios Zheng and Huang, 1986, p. 122

Holotype. IVPP V7642, portion of left mandible with P_4 - M_3 .

Referred Specimens. The type only.

Horizon and Locality. Wang-wu Member, Chi-jiang Formation; late Paleocene. North of Zhulin Hill, Dayu County, Jiangxi Province, People's Republic of China (cited from Zheng and Huang, 1986).

Diagnosis. Cheek-teeth lower-crowned than in *B. progressus*. Entolophid of lower molars not so well-developed as in that species and, at least on M_1 , incomplete; trigonid of lower molars more open lin-

gually, with the paracristid less truncated, than in *B. progressus*.

Bothriostylops progressus (Tang and Yan, 1976)

Figures 8, 9

Sinostylops progressus Tang and Yan, 1976, p. 92

Bothriostylops progressus Zheng and Huang, 1986, p. 127

Holotype. IVPP V4264.1, fragment of right mandibular ramus with M_2 .

Referred Specimens. The type, and IVPP 4264.2, right mandible fragment with worn M_{2-3} ; 4264.3, right mandible fragment with P_{3-4} ; 4264.4, right mandible fragment with P_{3-4} ; 4264.5, right mandible fragment with M_2 and with broken M_3 ; 4264.6, right maxillary fragment with broken M^1 and with M^{2-3} well-worn.

Horizon and Locality. IVPP locality 71071, Shuang-ta-si Group, Anhui Province, People's Republic of China; late Paleocene (Li and Ting, 1983) or early Eocene (Zheng and Huang, 1986).

Diagnosis. Cheek-teeth higher-crowned than in *B. notios*. Entolophid of lower molars complete and more fully developed than in that species; trigonid of lower molars more compressed, with paracristid more truncated, than in *B. notios*.

Anatolostylops Zhai, 1978, p. 109

Anatostylops, Schaff, 1985, p. 593

Type Species. *Anatolostylops dubius* Zhai, 1978, p. 109.

Included Species. The type only.

Distribution. Late early Eocene or early middle Eocene (*vide* Li and Ting, 1983) or, perhaps, Oligocene (*vide* Zhai, personal communication); Asia.

Diagnosis. Differs from all other genera, excepting an unnamed form, in having higher-crowned cheek-teeth; ectoloph of upper molars elongate, smooth and featureless, with a large parastyle but no parastylar fold. Pre- and postprotocristae salient, enclosing a fossette that persists through more advanced wear than in other forms. Sulcus on lingual side of M^2 crown

not so broad as in *Arctostylops* or *Palaeostylops*. Differs from a closely similar unnamed genus and species in having a lingual division of M^2 , and in lacking the great anteroposterior expansion of the ectoloph and the strong development of the postcingulum seen on upper molars of that genus.

Anatolostylops dubius Zhai, 1978, p. 109
Figure 8

Holotype. IVPP V4357, fragment of left maxilla with M^{2-3} .

Hypodigm. The type only.

Horizon and Locality. Shi-san-jian-fang Formation, Turpan Basin, Xin-jiang Province, People's Republic of China; Eocene or Oligocene (see above).

Diagnosis. As for the genus.

Asiostylops Zheng, 1979, p. 388

Type Species. *Asiostylops spanios* Zheng, 1979, p. 388

Included Species. The type only.

Distribution. Late Paleocene (*vide* Li and Ting, 1983), Asia.

Diagnosis. Distinct from all other arctostyloid genera in the more transverse P^{2-3} , with a lesser development of the protoconal region; upper molars lacking a posterolingual cusp or other secondary coronal complications; metaconid lacking on P_3 . Lower molars primitive in retaining the paracristid, as in *Bothriostylops* and *Sinostylops* but not other genera; cristid obliqua attaching to trigonid in a median position. Entolophid feebly developed and transversely oriented.

Asiostylops spanios Zheng, 1979, p. 388
Figures 8, 9

Holotype. IVPP V5042, cranium and associated left mandible.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 73039, Lan-ni-kong Member, Chi-jiang Formation, Jiang-xi Province, People's Republic of China.

Diagnosis. As for the genus.

Kazachostylops Nesov, 1987, p. 212

Type Species. *Kazachostylops occidentalis* Nesov, 1987, p. 212

Included Species. The type only.

Distribution. Late Paleocene, western Asia.

Diagnosis (from Nesov 1987, p. 211). Small arctostyloids with long, tall paracristid on lower molars; premetacristid and postmetacristid reduced to absent. Entolophid of M_{2-3} long, nearly transverse, and joined with the talonid loph. Crests of molar teeth form practically uninterrupted cutting edges.

Lacking access to the two, relatively good specimens of the type and only species of *Kazachostylops*, we defer to Nesov's brief diagnosis of the genus, and omit it from the detailed comparisons and discussion presented below. From the figures, *Kazachostylops* appears to be rather similar to *Bothriostylops* and, perhaps, *Sinostylops*, particularly in the elongate, well-developed M_3 , the strong, crescentic paracristid, and in the lingual attachment of cristid obliqua to trigonid (i.e., at the metaconid).

Kazachostylops occidentalis Nesov, 1987, p. 212

Holotype. Specimen number 10/12455, indicated by Nesov (1987) as being deposited in the Ts.N.E.G.R. Museum, Kazakhstan, Dzhalga, USSR, consisting of a right dentary with C, P_{3-4} , and M_{1-3} .

Hypodigm. The type, and at least one more dentulous jaw fragment figured by Nesov (1987), number 12/12455, consisting of a right maxilla with P^2 to M^1 .

Horizon and Locality. Marginal marine deposits of the Pretashkent Svita, late Paleocene; site TDA-2, Kazakhstan, Dzhalga, USSR (*vide* Nesov, 1987, p. 212)

Diagnosis. As for the genus.

Arctostylopidae?, incertae sedis
Allostylops Zheng, 1979, p. 391

Type Species. *Allostylops periconatus* Zheng, 1979, p. 391.

Included Species. The type only.

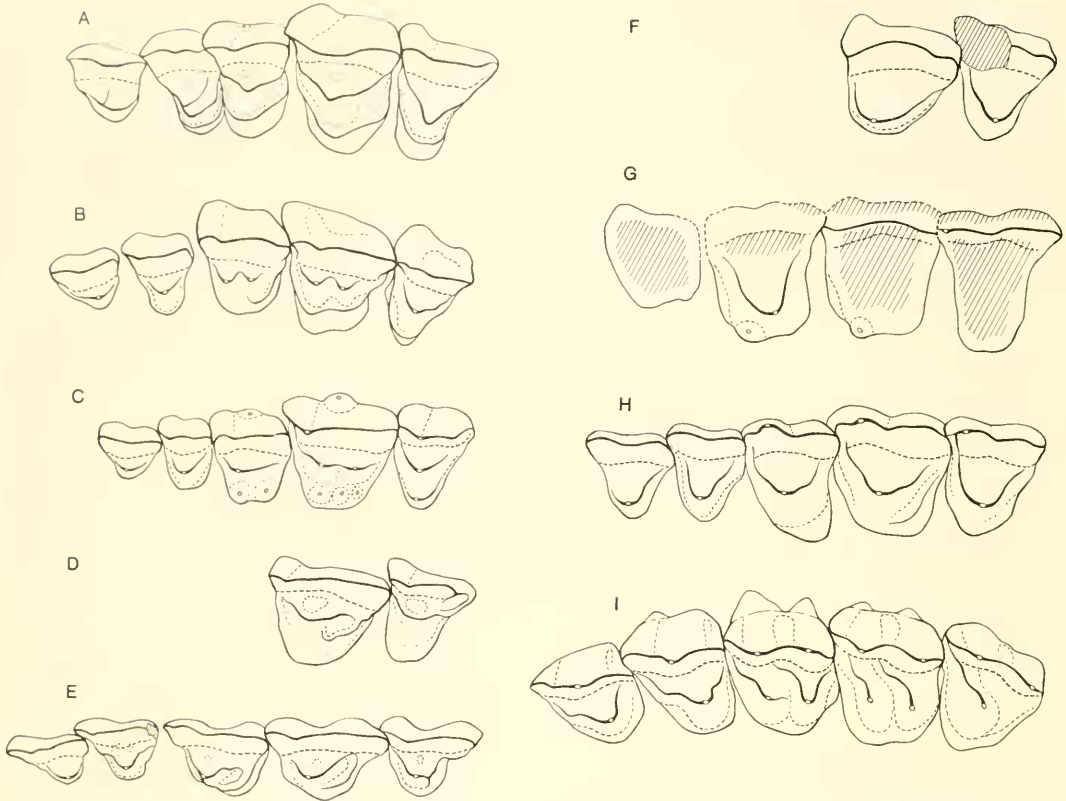


Figure 8. Comparative series of arctostyloid (A–H) and primitive notoungulate (I) upper dentitions. Teeth standardized to size and reversed where necessary. A, *Arctostylops steini* (MCZ 20004); B, *Palaeostylops iturus* (AMNH 22143); C, *Gashatostylops macrodon* (cast, AMNH 109521); D, *Anatolostylops dibius* (IVPP V4357); E, undescribed genus and species (unnumbered IVPP specimen); F, *Bothriostylops progressus* (IVPP V4264.6); G, *Allostylops periconatus* (IVPP V5043); H, *Asiostylops spanios* (IVPP V5042); I, *Peripantostylops minutus* (AMNH 28494).

Distribution. Late Paleocene (*vide* Li and Ting, 1983), Asia.

Diagnosis. Generally primitive ?arctostyloids similar to *Asiostylops spanios* in the low-crowned cheek-teeth, the small size of P³, and the presence of a paracone fold on the ectoloph of at least some upper molars, but differing from that species in hav-

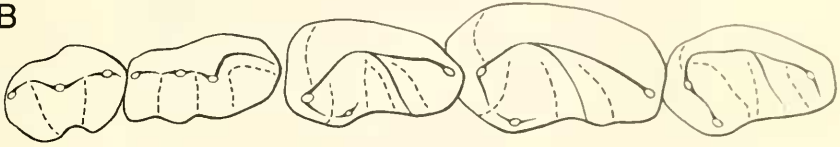
ing a hypocone on M². Differs from advanced arctostyloids (*Palaeostylops*, *Arctostylops*, *Gashatostylops*, *Anatolostylops*) in having lower-crowned cheek-teeth, a smaller P³, smaller upper parastyles, and a broadly expanded posterior cingulum on M¹. *Allostylops* is distinct from all forms in the family save

Figure 9. Comparative series of arctostyloid (A–E) and primitive notoungulate (F) lower dentitions. Teeth standardized to size and reversed where necessary. A, *Arctostylops steini* (MCZ 20004); B, *Palaeostylops iturus* (AMNH 20414); C, *Gashatostylops macrodon* (AMNH 21741); D, *Bothriostylops progressus* (P₃₋₄, IVPP V4264.4; M₂, IVPP V4264.1; M₃ outline, IVPP V4264.2); E, *Asiostylops spanios* (IVPP V5042); F, *Peripantostylops minutus* (AMNH 28494).

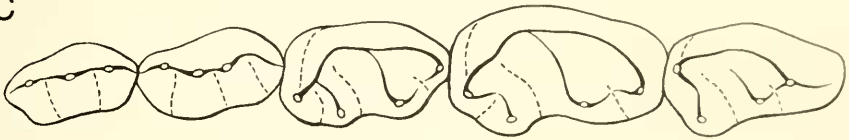
A



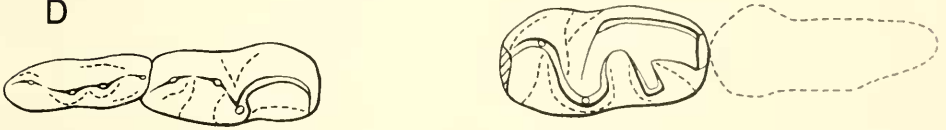
B



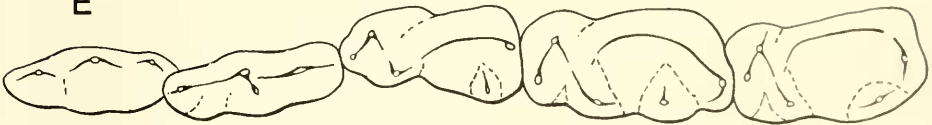
C



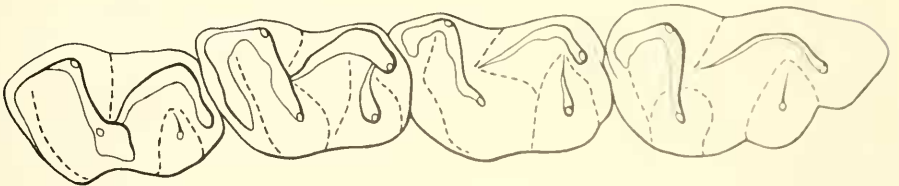
D



E



F



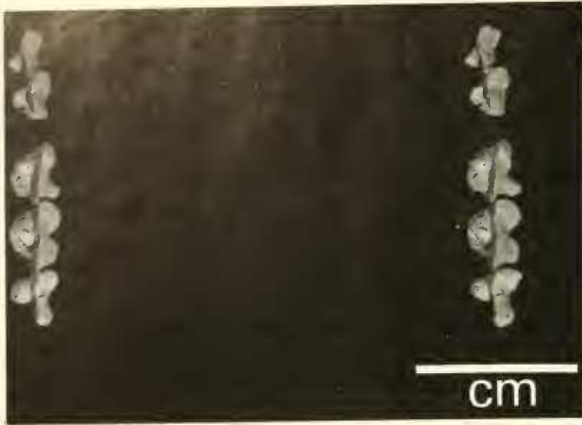


Figure 10. Stereophotographs of P^3 - M^3 of undescribed genus and species of Arctostylopidae (unnumbered IVPP specimen).

Gashatostylops in having a prominent pericone anterolingual to the protocone on upper molars.

Allostylops periconatus Zheng, 1979, p. 391

Holotype. IVPP V5043, badly preserved rostral portion of cranium.

Hypodigm. The type only.

Horizon and Locality. IVPP locality 73041, Wang-wu Member, Chi-Jiang Formation, Jiang-xi Province, People's Republic of China; late Paleocene.

Diagnosis. As for the genus.

Arctostylopidae, genus and species indet. A

In addition to the foregoing previously described species, an unnamed arctostylopid is represented by an upper dentition collected from the Yan-ma-tou Formation, Hunan Province, People's Republic of China. While full description of this species is in progress, we briefly note some of its morphological features here in order to facilitate comparison among other members of the family and to aid in assessing their relationships.

The taxon in question is a small, dentally advanced arctostylopid similar to *Anatostylops* in having high-crowned cheek-teeth and a smooth ectoloph on the upper molars, but it differs from this and all other

genera in the great anteroposterior expansion of the ectoloph crest on P^3 - M^3 and in the strong development of the postcingulum on M^{1-2} . Indeed, the ectolophs of the upper cheek-teeth are so strongly developed that the rest of each tooth appears by comparison to have been constructed as an afterthought. A lingual division of M^{1-2} , seen in all other genera except *Asiostylops*, is lacking. The second upper molar is notably larger than the first.

The single specimen representing this species was plotted into a measured section (Unit 21 of Zhu-chen, 1986) of beds reported to be of Cretaceous age. The basis for this surprising age determination is not entirely clear, but it seems to involve fossil remains believed to be dinosaur eggs (listed as *Elongatoolithus* and other taxa) which, apparently, bracket the arctostylopid specimen. Other fossils from this section are listed merely as "animal bones" or "animal teeth," and are therefore of little help in age determination. However, a mammalian axis vertebra is larger than that of any Chinese Paleocene mammal and would be totally out of place in the Cretaceous, as would a large anterior tooth of some ungulate-sized mammal. We believe on this basis that the locality is much younger than Cretaceous, perhaps even Eocene in age, whether dinosaurs were present or not. Indeed, the advanced mor-

phology of the small, distinctive arctostylopid from this site is suggestive of the Eocene or possibly Oligocene *Anatolostylops dubius*.

Arctostylopidae, genus and species indet. B

Another arctostylopid, which we have not seen, occurs in the late Paleocene Datanag Member of the Nung-shan Formation, Nan-xiong basin, Guang-dong, People's Republic of China. The animal is regarded as a new genus and species by Li and Ting (1983, p. 13).

COMPARATIVE DENTAL MORPHOLOGY OF THE ARCTOSTYLOPIDAE

Review of dental variations among the Arctostylopidae and assessment of the relative primitiveness of various character states is based on comparison with an ungulate morphotype as represented by *Protungulatum* and various comparable oxyclaenine Arctocyoniidae (Cifelli, 1983a). Some of the features that are represented in available materials of the known species are summarized in Table 4. The most primitive arctostylopid for which good materials are available is unquestionably *Asiostylops spanios* Zheng, 1979. Zheng (1979) referred *Asiostylops* to the Notoungulata based on the biselenodont lower molars, with shortened trigonid and lophodont entoconid, and on the upper molar ectoloph, with parastyle developed. He considered *Asiostylops* to be primitive within the order because the cheek-teeth are low-crowned, the premolars are not molarized (in particular, P_4 lacks an entoconid), the lower molars have a pronounced paraconid, and the upper molars lack the secondary coronal complications seen in *Henricosbornia* and more advanced South American notoungulates.

Compared to an ungulate morphotype represented by *Protungulatum*, *Asiostylops spanios* has a greater development of the protocone on P^{3-4} , with a metacone on those teeth; upper molars with an ectoloph

(strong, high centrocrista connecting paracone and metacone), strong, complete lingual cingula, indistinct conules, and reduced styler prominences; blade-like, serially tricuspidate P_3 , with notches separating the cusps; P_1 with a trigonid crest that is slightly curved (metaconid lingually placed) and a straight, short talonid crest, lower molars with a crescentic trigonid, paraconid in a median position, and a talonid consisting of cristid obliqua and postcristid united into a continuous crescent with hypoconid and hypoconulid indistinct. The entoconid of lower molars is isolated from the posteristid and developed into a faint, transverse loph which extends anterolabially to the talonid crescent. Many of these features are shared by presumably unrelated groups of mammals, but the serially tricuspid anterior lower premolars and the transversely developed entoconid (entolophid) of the lower molars are rather distinctive characters.

Arctostylops, *Palaeostylops*, and *Gashatostylops* are distinctively more specialized. Advanced characters of these three genera with respect to *Asiostylops* include higher-crowned posterior premolars and molars; an expanded protocone on P^3 ; upper molars with a high, flat ectoloph wall including parastylar and metastylar folds only (*Asiostylops* has a distinct paracone fold); M^2 , at least, is bifid lingually, with high pre- and postprotocristae that enclose a very transient trigon fossette but which are rapidly reduced by heavy wear. The lower molars of these three genera are distinctive in a number of respects, such as: 1) the presence of a salient, pillar-like, ectocingulid with a wear surface descending along its face; 2) the reduction of the trigonid by loss of the paracristid; 3) the presence of a high, shearing talonid crescent (cristid obliqua), which joins the trigonid labial to position of the protoconid; and 4) the strongly developed, oblique entolophid. All three genera have an anteriorly placed P_4 paraconid, unlike *Asiostylops*. The polarities of some features of P_4 are uncertain. *Arctostylops* differs from

Palaeostylops, *Gashatostylops*, and most other Arctostylopidae in the presence of a crescentic P_4 talonid loph, and differs from *Gashatostylops macrodon* (but not *Palaeostylops iturus* and several other species) in the lingual placement of its P_4 metaconid. *Arctostylops steini* is probably autapomorphic in having a stronger ectocingulid on P_{3-4} , a stronger lingual rib on C_1 , a prominent heel on I^1 , and a slightly larger protocone on P^2 . *Palaeostylops* and *Gashatostylops* appear to be derived with respect to *Arctostylops* in the lesser differentiation of C^1 , the lack of paracone folds on the ectoloph of P^{3-4} , and the presence of a shearing notch on P_4 . *Palaeostylops* and *Gashatostylops* differ from *Arctostylops* also in the more quadrate, less transverse nature of M^{1-2} and in the fact that the sulcus between the two internal cusps is better developed, at least on M^1 . The P_4 cusps in *Gashatostylops macrodon* are more or less anteroposteriorly aligned, as with the more anterior premolars of all genera; the talonid crest is a straight, bladelike structure. *G. macrodon* is also distinctive in that the upper and lower second molars are greatly enlarged, in the variable development of one or more cusps on the lingual cingulum, and in the reduction or absence of a lingual sulcus on M^1 (further distinctions are given in the diagnoses provided above). Thus, *Arctostylops*, *Gashatostylops*, and *Palaeostylops* share presumed synapomorphies with respect to *Asiostylops*. Within this clade of advanced genera, there is some evidence to suggest that *Gashatostylops* and *Palaeostylops* shared a more recent common ancestor than either did with *Arctostylops*. Because of uncertainty in morphocline of several features, the possibility of lineal relationships between any of the included species cannot be evaluated.

The remaining species of Arctostylopidae are known from less complete materials and there is, accordingly, some uncertainty as to various character states. Although rather primitive, the two species of *Bothriostylops* are unique among arc-

tostylopid in having an elongate M_3 in which the hypoconulid forms a separate lobe. (This also appears to be true of lower molars belonging to *Kazachostylops occidentalis*, which we have not examined firsthand. We are unable to consider the species further here, but note that the above-mentioned feature and several other lower molar characters suggest a close relationship to *Bothriostylops* spp.) We assume, for the purpose of comparison, that these two species form an exclusive unit within the family. Thus conceived, *Bothriostylops* is, in several respects, intermediate between *Asiostylops* on the one hand and advanced arctostylopid (Arctostylops, *Gashatostylops*, *Palaeostylops*) on the other. As in *Asiostylops*, *Palaeostylops*, and *Arctostylops*, the metaconid on P_4 is lingually placed (we are uncertain of the condition in *B. notios*). The talonid crest of that tooth is curved in *Bothriostylops* spp, although not so strongly as in *Arctostylops*. The lower molar trigonids of *B. progressus* are anteroposteriorly compressed, as in the derived genera, but unlike those forms, part of the paracristid remains, as in *Asiostylops*. In *B. notios*, the trigonid retains a more open arrangement, with the paracristid little reduced. The cristid obliqua attaches to the trigonid at a lingual position, near the apex of the metaconid, unlike either *Asiostylops* on the one hand or *Palaeostylops*/*Arctostylops* on the other. The ectocingulid is feebly developed and not expanded into an occlusal structure. The entolophid varies from well-developed (*B. progressus*), as in the advanced forms, to weak and incomplete (*B. notios*). A partial, very worn, upper molar series is available for *Bothriostylops progressus*, but it adds little to knowledge of the species. The ectoloph appears to have been high; as far as can be determined, paracone and metastylar folds are lacking although a parastylar fold is well-developed. M^1 has a sulcus separating two lingual cusps; this appears not to have been true of M^2 , which is triangular in outline (as with *Asiostylops*), but excessive wear has obscured de-

TABLE 4. DENTAL CHARACTER COMPARISONS AMONG THE ARCTOSTYLOPIDAE.

Character	<i>Asio spurius</i>	<i>Sino promissus</i>	<i>Bothrio. nottus</i>	<i>Bothrio. progressus</i>	<i>Arcto. steni</i>	<i>Palaeo. iturus</i>	<i>Gashato. macradon</i>	<i>Anatol. dithus</i>	Undescr. Taxon
P ₃ metaconid	absent	present	?	present	present	present	present	?	?
P ₄ metaconid	lingual	?	lingual	lingual	lingual	lingual	lingual	?	?
P ₄ talonid	straight	?	curved	curved	curved	notch	shearing notch	?	?
P ₁ paraconid	lingual	?	?	lingual	labial	labial	labial	?	?
P ₁ ectocingulid	absent	?	?	faint	strong	faint	faint	?	?
M ₁ ectocingulid	absent	present	present	present	pillar	pillar	pillar	?	?
M cr. obliqua	medial	lingual	lingual	lingual	labial	labial	labial	?	?
M ₁ entolophid	weak/abs.	?	weak/abs.	strong	strong	strong	strong	?	?
M ₁ paraeristid	present	present	present	present	absent	absent	absent	?	?
M ₃ hyd lobe	absent	?	present	present	absent	absent	absent	?	?
Enlarged M ₂	absent	absent	absent	absent	absent	absent	present	present	present
Crown height	low	moderate	moderate	moderate	high	high	high	v. high	v. high
p3-4 pa fold	present	?	?	?	present	absent	absent	?	absent
M pa fold	present	?	?	absent	absent	absent	absent	absent	absent
M ₁ parastyle	small	?	?	large	large	large	large	v. large	v. large
M pas fold	present	?	?	present	present	present	present	absent	absent
M ling. sulcus	absent	?	?	M ₁	M ₁₋₂	M ₁₋₂	M ₂ , sm. M ₁	?	absent
M ₁₋₂ cingulum	incomplete	?	?	complete	complete	complete	complete	complete	complete
M ₁ ectoloph	low	?	?	high	high	high	high	high, long	high, long
M protoeristae	weak	?	?	?	strong	strong	strong	v. strong	v. strong

tails of crown morphology. M^2 may have been slightly larger than the adjacent teeth, but it is not greatly enlarged as in *Gashatostylops macrodon*.

As for *Sinostylops promissus* Tang and Yan, 1976, poor preservation of the type and only known specimen leaves various character states open to question. It cannot be determined if an entolophid was present on M_{1-2} . It appears that a trigonid crescent was retained, as in *Asiostylops*, and the cristid obliqua attaches to the trigonid at the metaconid, as in *Bothriostylops* spp. The antemolariform teeth form a graded series and are long, narrow, and bladelike, especially dP_4 . The premolars are serially tricuspid, with a straight, crested heel. *Sinostylops promissus* lacks advanced features of the lower molars seen in *Palaeostylops* and *Arctostylops*. The morphology of the premolars would seem to indicate pertinence to the Arctostylopidae; within the family, *Sinostylops promissus* is similar only to *Bothriostylops* spp. in the lingual attachment of cristid obliqua to trigonid.

Allostylops periconatus Zheng, 1979, about which little can be said, is represented by the rostral part of a skull with the dentition very poorly preserved. The upper molars resemble those of *Asiostylops*, and are therefore presumably primitive, in lacking an enlarged parastyle and in retaining paracone and metacone folds on the ectoloph. There was, apparently, no posterointernal cusp on M^{1-2} ; a prominent anterolingual cusp (pericone) is present on the lingual cingulum, as is variably present on upper molars of *Gashatostylops macrodon*. The posterior cingulum of M^{1-2} is broadly expanded, so that the molars are subquadrate in occlusal aspect. The dentition as preserved gives little indication of affinity to this group, and the position of *Allostylops* is therefore indeterminate.

Anatolostylops dubius Zhai, 1978, known from M^{2-3} , is clearly a rather specialized form and may be significantly younger than the other genera. As in *Palaeostylops*, *Arctostylops*, *Gashatostylops*, and *Bothriostylops*, the ectoloph is high

and lacks a paracone fold; unlike those forms, the ectoloph is otherwise featureless, lacking a parastylar fold or basal bulges in the regions of parastyle and metastyle. The lingual coronal crests (pre- and post-protocristae) are strong and enclose a fossette that probably persists into a fairly advanced stage of wear. The sulcus between the lingual cusps on M^2 is not so deep as in *Palaeostylops* or *Gashatostylops* but, as in those genera, it probably persists to advanced wear. A lingual cingulum is weak or lacking on M^3 , as in *Bothriostylops progressus*; as in *Gashatostylops macrodon*, M^2 is considerably larger than M^3 . *Anatolostylops* is most closely similar to the unnamed genus and species, with which it shares several derived characters not found in other Arctostylopidae. The ectoloph is anteroposteriorly elongate, with labial plications reduced or lost. The lingual division of upper molars is poorly marked in *Anatolostylops* and absent in the unnamed form; because these genera otherwise appear to be closely related to forms in which it is well-developed (e.g., *Palaeostylops*), we believe this to represent reduction or loss rather than retention of a primitive condition (as in *Asiostylops*). The cheek-teeth of the undescribed genus and *Anatolostylops* are higher-crowned than in other genera, and the pre- and postprotocristae better developed, enclosing a more persistent fossette than in other members of the family. Although *Gashatostylops* is autapomorphic in several respects, notably in the development of accessory cuspules on the lingual cingulum and base of the ectoloph of upper molars, it is similar to *Anatolostylops* and the undescribed form in several other respects. These include a reduction of the lingual sulcus on at least the first tooth of the upper molar series and the great size of the second molar relative to that of adjacent teeth.

Among advanced Arctostylopidae, *Anatolostylops* is divergent in having double opposition of upper to lower teeth, as indicated by the presence of a distinct wear facet in the mesostylar area of the upper molar (this would correspond to a facet

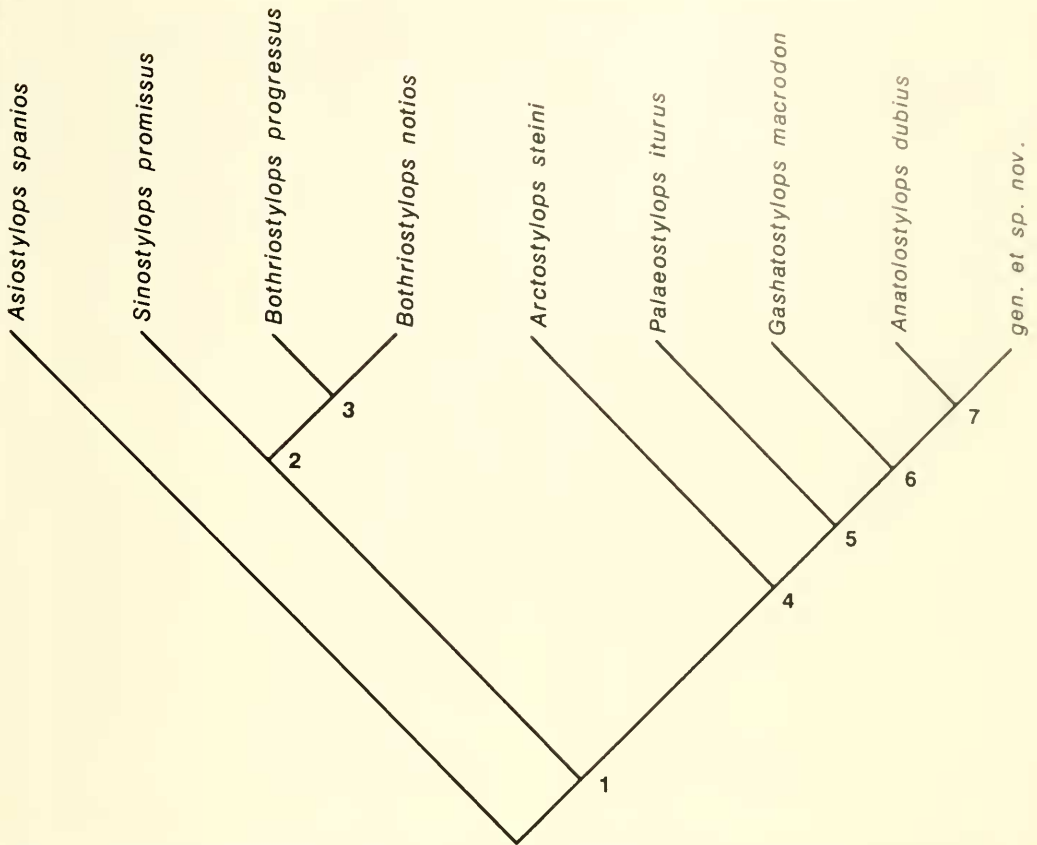


Figure 11. Hypothesized relationships among the Arctostylopidae. Characters at nodes (see Table 4): 1) metaconid added to P_3 , pseudohypocone on at least one upper molar, upper molar paracone fold lost, ectocingulid developed on lower molars, ectocingulid developed on P_4 , P_4 talonid curved, upper molar parastyle enlarged; 2) lower molar cristid obliqua attaches lingually to rear of trigonid; 3) M_3 elongate? (condition unknown in *S. promissus*); 4) lower molar entolophid well developed, lower molar cristid obliqua attaches labially to rear of trigonid, lower molar ectocingulid strong and pillarlike, P_4 paraconid shifted labially, lower molar paracristid lost; 5) shearing notch developed on P_4 talonid, P^{3-4} paracone fold lost, canines lesser differentiated; 6) second molars enlarged, pseudohypocone lost on M^1 ?; 7) upper molar protocristae salient, M^2 pseudohypocone reduced?, parastyle fold on ectoloph of posterior upper cheek teeth lost, ectoloph of upper molars anteroposteriorly elongate, cheek teeth very high crowned.

anterior to the protoconid on the lower molars, which are not known for *Anatolostylops*). This facet is lacking in *Arctostylops*, *Palaeostylops*, and *Gashatostylops*, which apparently had singly opposing upper and lower cheek teeth.

An hypothesis of interrelationships of the Arctostylopidae is given in Figure 11⁷ (*Kazachostylops occidentalis*, which we have not examined first-hand, and *Allostylops*

periconatus, poorly known and of doubtful affinities, have been omitted from this phylogeny). *Asiostylops spanios* is the most primitive taxon known and is considered to represent the sister group of all remaining taxa. *Bothriostylops* spp., unique in at least one character (the presence of a hypoconulid lobe on M_3), generally resemble *Asiostylops* in their retention of primitive features, but nonetheless appear to share several derived features with the remaining taxa. Among these are the presence of a P_3 metaconid, a curved P_4 talonid, a lingual division of M^1 , and the loss of the

⁷ The absence of a chronologic dimension is due to uncertainties of relative age, not our lack of appreciation for this consideration.

paracone fold and the presence of a large parastyle on the upper molars. *Sinostylops promissus* (poorly known and lacking much of the most diagnostic morphology in the type and only specimen) is similar only to *Bothriostylops* spp in its lingual cristid obliqua-trigonid attachment; it is very tentatively regarded as the sister taxon of *Bothriostylops* spp. The remaining Arctostylopidae clearly are united by derived morphology not found in *Asiostylops* or *Bothriostylops*. These features include mainly specializations of the lower cheek-teeth, such as the labial attachment of the cristid obliqua, the presence of a pillar-like ectocingulid, and the loss of the paracristid. Among advanced genera, *Arctostylops* appears to be the most primitive, lacking specializations such as a shearing notch on P_3 , found in *Palaeostylops* and *Gashatostylops*. Within the group formed by the remaining genera, the undescribed form and *Anatolostylops* possess several synapomorphies (mainly features related to the hypertrophied ectoloph of upper molars) and both share with *Gashatostylops* an enlarged second molar.

THE NOTOUNGULATA OF SOUTH AMERICA

The early Tertiary Notoungulata of South America have been fully reviewed by Simpson (1948, 1967). Additions to knowledge since publication of these monographs have been principally the Itaboraian to Casamayoran notoungulates of Itaboraí, Brazil (Paula Couto, 1952, 1954, 1978) and of northwestern Argentina (Bond, 1981; Pascual, Vucetich, and Fernandez, 1978; Vucetich, 1980). As recognized by Simpson, the major advanced notoungulate suborders Toxodonta and Typotheria (including Hegetotheria; see Cifelli, 1985a) were differentiated by the late Paleocene, with 5 families collectively represented. Simpson grouped two other families of the earliest faunas (Riochican and Casamayoran), the Henricosborniidae and Notostylopidae, into his paraphyletic suborder Notioprogonia. When compared

with an ungulate morphotype, of which *Protungulatum* is a good approximation, all these notoungulates of the earliest faunas share a number of dental specializations (Figs. 8I, 9F). The posterior upper premolars (P^{3-4}) are somewhat molarized, with large protocones supporting anterior and posterior lingual cingula and trigonal crests; the teeth are dominated labially by a prominent paracone, which is separated from the also well-developed parastyle and metastyle. A metacone, as far as is known, does not develop on upper premolars of notoungulates. Illustrated specimens of *Henricosbornia lophodonta* (Simpson, 1948, figure 53) and *Oldfieldthomasia debilitata* (Simpson, 1967, plate 5) have metacones on the teeth indicated to be P^4 , but comparison with other materials belonging to these species indicate that the teeth in question are probably deciduous. The upper molars bear a strong ectoloph whose labial wall is marked by sulci separating parastyle, paracone, and metacone. M^{1-2} are quadrate in occlusal view, with a posterolingual cusp (hypocone) separated from the protocone by a sulcus. M^3 does not develop a hypocone, but variants among even primitive taxa may show strong development of the cingulum in this region. The crest linking protocone to paracone (preprotocrista) is strong and is developed into a protoloph; on the first two molars, at least, and variably on M^3 , a metaloph joins hypocone and metacone (Fig. 12). The metaconule of upper molars is expanded anterolabially into the trigon basin as a crochet; various other cusps and crests characterize this part of most notoungulate upper molars (see Patterson, 1934; Simpson, 1948). Cingula are present anteriorly and posteriorly but not lingually. The posterior lower premolars (P_{3-4}) are molarized (P_3 somewhat less than P_4); the trigonid is crescentic, with crests directed anteriorly and posterolingually from the protoconid; the talonid is much shorter than the trigonid and also bears a crescentic crest. The construction of the lower molar trigonids is extraordinary, and the homol-

ologies of some parts are open to question. A crest (paracristid?), variable in length, extends anteriorly or anterolingually from the protoconid; a low anterior crest or cingulum, on the anterior face of the tooth, may connect with this in heavy wear so that the paracristid (?) appears to run to the lingual margin of the tooth. The greatest variation occurs in the region of the metaconid. That cusp may be anteroposteriorly expanded (Henricosborniidae, some Oldfieldthomasiidae), bearing an anterolabial-posterolingually directed crest. Another variant involves the presence of an anterior accessory cusp, which sometimes bears the appearance of a paraconid that has lost the paracristid connecting it to the protoconid (most notably in Isotemnidae but also in some Oldfieldthomasiidae). Notostylopids are characterized by an accessory cusp on the crest linking protoconid to metaconid (protocristid), so that this crest is serially tricuspid. Marshall, de Muizon, and Sigé (1983) propose homologies for these trigonid structures, which they argue are variations about a basic notoungulate pattern that included a pre- and postmetastylid. The talonid consists, in its simplest form (Henricosborniidae), of a crescent (cristid obliqua and posteristid) uniting hypoconid and hypoconulid, which nonetheless are retained as distinct, cusp-like entities. The entoconid is developed transversely (entolophid) and, in advanced forms, joins the posteristid anterior to the hypoconulid. The most primitive condition of this feature is seen in henricosborniids such as *Henricosbornia* itself. The entolophid is incompletely developed, posterobuccally oriented, and is somewhat more separated from the hypoconulid on the posteriormost molar of Henricosborniidae. On M_1 , however, this crest runs labially to the hypoconulid or to a point just anterior to that cusp, and it therefore appears that the entolophid is homologous to the crest connecting entoconid and hypoconulid (a portion of the posteristid), and becomes distinct as a separate loph by migrating anteriorly.

DISCUSSION

In the original description of the species, Matthew (1915) referred *Arctostylops steini* to the order "Entelonychia" and, within that group, placed the species with some doubt in the Isotemnidae. At that time, "notoungulate" to many students (see, e.g., the influential classifications of Gregory, 1910; Osborn, 1910; and Scott, 1904) was equivalent to "indigenous South American ungulate," and did not explicitly refer to that group in the sense it is defined today⁸. "Entelonychia" was a suborder proposed by Ameghino (1894) to include the aberrant, clawed *Homalodotherium* (a Santaacrucean, mid-Miocene form shown by Patterson, 1936, to be toxodont-like in the construction of its ear region and since universally placed in the Toxodonta, a suborder of the Notoungulata) within the "Ancylopoda," thus uniting it with the similarly clawed chalicotheres of Holarctic faunas. Ameghino had abandoned the use of the term "Entelonychia" by the time of his final (1906) classification, but by this time had placed other notoungulate families (Isotemnidae and Leontiniidae, both currently recognized as belonging to the Toxodonta) with the Homalodotheriidae in the "Ancylopoda." The dentition of members of all these families are relatively primitive within the Notoungulata. Thus, later workers ignored Ameghino's reference of these and other notoungulates to Holarctic groups, and instead resurrected his term "Entelonychia" to include generally primitive notoungulates. (Scott, 1913, for instance, placed the Notostylopidae under this heading.) At the time of Matthew's (1915) writing, "Entelonychia" referred to primitive notoungulate mammals; then, as now, the Isotemnidae were considered to be basal members of the South American notoungulate radiations (although the henricosborniids are generally acknowledged to be somewhat more primitive).

⁸ The concept of the Notoungulata now current had, however, been made clear by Roth, 1903.

Matthew and Granger (1925) recognized that *Palaeostylops iturus* was strongly specialized in having high-crowned cheek-teeth with well-developed shearing surfaces, and in having reduced lower molar trigonids. In this respect, they indicated that (pp. 4-5), "it may be regarded as ancestral to *Arctostylops* and through that genus to some of the South American Eocene Notoungulata (e.g., *Leontinia*, *Notostylops*, etc.) but to the latter only in a broad way, as no one of the genera of the Deseado fauna can be cited as clearly following the line indicated by *Palaeostylops-Arctostylops*." Nonetheless, as implied in the foregoing statement, they regarded *Palaeostylops* as more primitive in a number of features (for instance, the simple premolars) than the earliest of the South American notoungulates or *Arctostylops*. They thus believed the Asian genus to be ancestral, at least in a general sense, to all New World forms, and that "the South American Tertiary hoofed mammals were originally derived from the north, although undergoing a great secondary evolution in the Neotropical region" (p. 2).

Simpson (1934) clearly defined the Notoungulata and its contents. He removed the Arctostylopidae and Notostylopidae (a group of primitive South American notoungulates) from the "Entelonychia" and placed them with the Henricosborniidae in a then new paraphyletic suborder, Notioprogonia, defined on the basis of primitiveness of its constituent taxa. This left the "Entelonychia" as Ameghino had originally conceived it except that Simpson removed the Leontiniidae to the Toxodonta. Thus recognized, the Notoungulata comprised four suborders: Notioprogonia, "Entelonychia," Toxodonta, and Typotheria. On the basis of further studies (Patterson, 1936; Simpson, 1936b), Simpson later (1945) removed the remaining contents of the "Entelonychia" (Isotemnidae and Homalodotheriidae) to the Toxodonta, where they have since remained.

Simpson's view, elaborated in his two memoirs devoted to the earliest South American mammal faunas (Simpson, 1948,

1967), was that the Henricosborniidae, then known only from the Riochican and early Casamayoran (Cifelli, 1985b), or putative late Paleocene and early Eocene (Marshall, 1985; Marshall, Hoffstetter, and Pascual, 1983), represent the most primitive of known Notoungulata. By this interpretation, the order arose in South America from the same "ungulate" stock which gave rise also to the other groups of indigenous South American ungulates. Migration of a primitive notoungulate to North America and thence to Asia would thus provide the source for the Arctostylopidae (Simpson, 1951, 1965, 1978, 1980). Szalay and McKenna (1971) followed Simpson in this respect, noting that molars of then known arctostylopids were more advanced than any in the earliest South American notoungulates. Apparent support for a southern origin of the Notoungulata, on both morphological and temporal grounds, is lent by the proposed referral of *Perutherium*, from the Late Cretaceous of Peru, to the order (Marshall, de Muizon, and Sigé, 1983). Placement of this genus, which is based largely on two broken molars of the type and only species, has been a matter of considerable dispute since its initial description (Grambast *et al.*, 1967), with workers variously suggesting arctocyonid (Grambast *et al.*, 1967), didolodontid (Tedford, 1974), peripitychid (Van Valen, 1978), and even marsupial (Hoffstetter, 1981) affinities. Marshall, de Muizon, and Sigé (1983) suggested that *Perutherium* possesses, in common with notoungulates, a pre- and postmetastylid in the trigonid of the lower molars, and that the genus is a morphologically appropriate antecedent to both the South American notoungulates and the Arctostylopidae.

Patterson (1958; Patterson and Pascual, 1972), on the other hand, followed Matthew (1928; Matthew and Granger, 1925) in believing that notoungulates arose in the north and, along with several mammalian companions, colonized South America in the earliest Tertiary, later to radiate and flourish on that continent. The basis for this opinion is unclear, but it is likely that

Patterson, like Matthew before him, was impressed by the early records of Arctostylopidae in North America (then thought to be early Eocene) and Asia (latest Paleocene), and by several of the strikingly primitive dental features found in members of that family. An Asian origin for the Notoungulata was also suggested by Nesov (1987). Gingerich and Rose (1977) proposed yet another possibility, that the Notoungulata arose in Central America (where evidence bearing on this issue is lacking) and from there spread both northward and southward.

Because of the inferred primitiveness of *Asiostylops* within the Notoungulata (simple premolars, triangular upper molars lacking a hypocone, simple molar lophs, unreduced anterior wing of lower molar trigonids), Zheng (1979) suggested that the order originated in Asia and, more specifically, in southern China. Earliest records need not infallibly indicate centers of origin, however. Van Valen (1988) considered *Asiostylops* to be sufficiently primitive to be structurally antecedent to trigonostylopid (an archaic group of Astrapotheria, which are endemic to South America).

Several recent studies have emphasized the profound differences in dental specializations between the Notoungulata and the Arctostylopidae, and on this basis have tentatively disassociated Holarctic from South American forms (Cifelli, 1983a, 1985a; Schaff, 1985; Thenius, 1985). It is well worth pointing out that it was Simpson who first flirted with this possibility, before returning to a more traditional view in the same paper:

“A possibility that seems not to have been considered but perhaps should be is that *Arctostylops*, *Palaeostylops*, and *Sinostylops*, although quite surely related among themselves, might not after all be true notoungulates. Their dentitions do have derived characters that occur in almost all early notoungulates with various modi-

fications and some marked changes in later, more specialized forms. These apparently diagnostic characters are not known in any other defined order of mammals. Nevertheless, these are unlike South American notoungulates in detail and one cannot absolutely exclude the possibility of convergence.” (Simpson, 1978, p. 325)

Possible Relationships

Evaluation of these contrasting views on the origin and subsequent dispersal of the Notoungulata, of great interest in both zoogeographical and paleobiological terms, is dependent on determination of morphocline polarity sequences and the robustness of the phylogenetic framework derived therefrom. The issue of fundamental interest, one which remains to be examined in detail, is the phylogenetic position of the Arctostylopidae with respect to South American Notoungulata. Assuming notoungulate monophyly, inclusive of the Arctostylopidae, three possibilities present themselves: 1) arctostylopid took origin from a southern notoungulate as that group is known (southern origin); 2) the southern notoungulates derived from a form that falls within the Arctostylopidae as that group is here conceived (northern origin for the order); and 3) the Arctostylopidae and known South American Notoungulata are sister taxa (northern or southern origin).

Even without knowledge of the cranial morphology of arctostylopid (a suite of synapomorphies characterizes this region in notoungulates; Simpson, 1948), there is rather imposing evidence, in the dentition and proximal ankle, that the southern Notoungulata constitute a monophyletic assemblage. Derivation of the Arctostylopidae from within the order as it is currently recognized would require many simplifications (reversals) in the dentition, because *Asiostylops* in many cases and all arctostylopid in some instances are more primitive than any known southern notoungulate. The most significant of these

characters are in the upper molars. All southern notoungulates have secondary complications, consisting of at least a crochet (Patterson, 1934; Simpson, 1948) in the trigon basin on all upper molars and a hypocone on M^{1-2} ; all arctostylopids lack the first character and at least *Asiostylops* among that family lacks either a hypocone or hypocone-like structure. By analogy with a series of variants in M^3 of *Henricosbornia lophodonta* (Fig. 12), which are not quadritubercular but which illustrate a plausible character state series for the addition of the posterolingual cusp on primitive notoungulate anterior upper molars, the posterointernal cusp of southern notoungulates appears to be a derivative of the cingulum and therefore a "true" hypocone (Simpson, 1929). By contrast, in arctostylopids which have quadritubercular M^{1-2} , the posterointernal cusp is encircled basally by the cingulum and appears to have originated as a transverse, lingual extension of the metacrista from the region of the metaconule⁹. Thus, the posterolingual upper molar cusp of southern notoungulates and arctostylopids appears to have been acquired independently and in a nonhomologous fashion.

Even the most primitive of southern Notoungulata (Henricosborniidae) have submolariform posterior lower premolars; P_4 has a complete, curved talonid crescent. Although the serially multicuspate, blade-like lower premolars of such forms as *Palaeostylops* may reflect specialization for shearing (secondary simplification), *Asiostylops* lacks the degree of molarization seen even in henricosborniids.

The proposed addition of *Perutherium altiplanense* to the Notoungulata (Marshall, de Muizon, and Sigé 1983) presents further problems for an origin of the Arctostylopidae within that group. Marshall,

de Muizon, and Sigé (1983) suggest that the various accessory trigonid structures of notoungulates may be homologized with a pre- and a postmetastyloid and that these are primitive for the order. Unlike typical South American notoungulates and the Arctostylopidae, *Perutherium* lacks an entolophid on its lower molars. The absence of a pre- and postmetastyloid in *Asiostylops* and *Bothriostylops* would therefore require postulation of secondary loss of these structures in forms which otherwise seem to be rather primitive in the construction of their lower molars. Thenius (1985) accepted the lower molar pre- and postmetastyloid pattern as a synapomorphy of notoungulates, and excluded arctostylopids from the order because it was lacking from "*Palaeostylops steini*."

The morphotype for the notoungulate proximal ankle bones is not strongly specialized (as compared, for instance, to ungulate groups such as the Litopterna, Perissodactyla, Artiodactyla, and Hyracoidea, all of which are highly modified at first appearance in the fossil record). Nonetheless, it is characterized by a number of synapomorphies which render it readily recognized (Cifelli, 1983b). These features include a long, constricted astragalar neck, with an oblique dorsal crest; astragalar body with a median (tibial) protuberance; astragalar foramen with posterolateral sulcus interrupting continuity of tibial trochlea and flexor tendon groove; and well-developed sustentacular-navicular facet contact on the astragalus.

Except for a constricted astragalar neck, none of these features is shared with known arctostyloid ankle regions (*Gashatostylops macrodon* and *Palaeostylops iturus*), which bear specializations contrasting with those of notoungulates. The arctostyloid ankle is advanced in having an astragalus with a cylindrical, vertically-walled body, the tibial trochlea extensively developed anteroposteriorly; lack of a fibular shelf; navicular facet developed so that the axis of movement along the midtarsal joint would have been roughly parallel (rather

⁹Cifelli (1983a, p. 40) considered the posterointernal cusp of arctostyloid upper molars to be a displaced and transversely expanded metaconule; it appears, however, that the upper molar conules were lost early on in arctostyloid evolution.

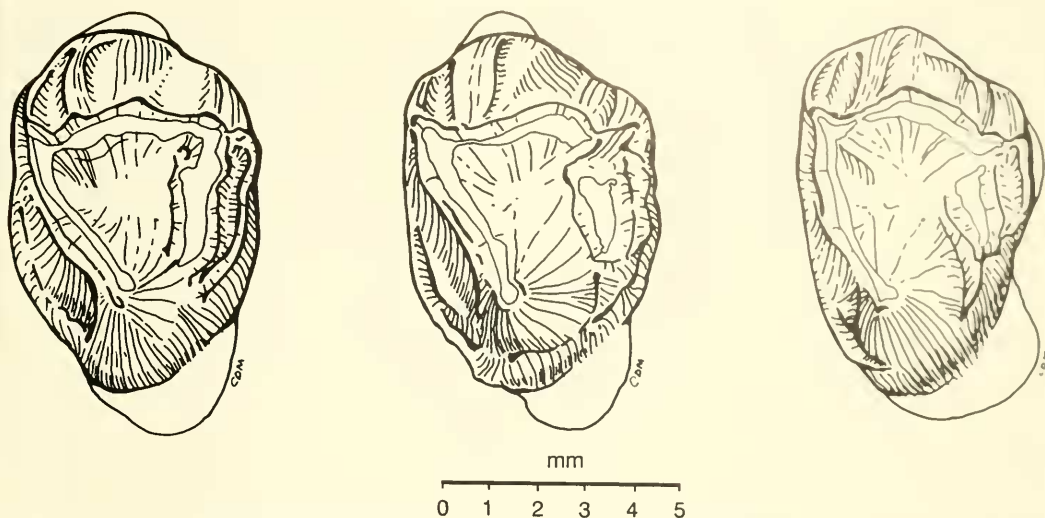


Figure 12. M^3 variants in *Henricosbornia lophodonta*, AMNH 28964, from the early Casamayoran Cañadon Vaca local fauna, illustrating hypothesized addition of hypocone through linking of postcingular cusp and metaloph.

than oblique) to that at the proximal ankle joint; astragalar cuboid facet lost (?); ectal facet steeply inclined with respect to inferior surface of astragalus; calcaneal fibular facet strongly developed into a semi-cylindrical surface; and sustentaculum of calcaneus distally located, at or near distal (cuboid) end of the bone. Most of these ankle modifications are usually associated with restriction of lateral and inversion/eversion movement, with concomitant greater capability for flexion/extension, at the proximal and mid-tarsal joints. Such specializations are commonly found among terrestrial mammals (Cifelli, 1983b). The extreme distal position of the astragalo-calcaneal facets on the calcaneus (a primitive condition?), implying poor mechanical advantage for rapid flexion of the pes by the gastrocnemius and soleus muscles, is enigmatic in this regard, and contrasts with the condition seen in terrestrial saltators or cursors. In any event, regardless of the paleobiological implications of this unusual ankle morphology, it is clear that notoungulates are uniquely derived with respect to arctostyloids, and vice versa.

Derivation of southern notoungulates from the Arctostyloidae (Matthew and

Granger, 1925; Patterson, 1958; Zheng, 1979) is also contradicted by the available morphological evidence. Neotropical Notoungulata have a different style of upper premolar molarization from that of arctostyloids and lack a metacone on P^{3-4} . The lower molars of henricosborniids show a very primitive state in the development of the typical notoungulate talonid: the major cusps (entoconid, hypoconid, hypoconulid) remain distinct; the entolophid is weak. The placement and orientation of the entolophid suggest that it was derived from the entoconid to hypoconulid part of the posteristid. Even in primitive arctostyloids (e.g., *Asiostylops*), the hypoconid is indistinct, having been merged into the talonid crescent. The entolophid of arctostyloids is advanced in being more anteriorly placed and is oriented anterolaterally (Schaff, 1985). If *Perutherium* is a notoungulate, as argued by Marshall, de Muizon, and Sigé (1983), then derivation of South American taxa from arctostyloids would require independent acquisition of the entolophid in the Neotropical forms, because that structure is lacking in *Perutherium*.

The final possibility is that known Arc-

tostylopidae and southern Notoungulata are sister taxa: that they shared an ancestor that was exclusive to them and no other group of mammals. This hypothesis would be compatible with all existing scenarios regarding the geographic origin and dispersal of notoungulates. With the addition to the Arctostylopidae of primitive forms such as *Asiostylops* and *Bothriostylops*, nearly all of the similarities shared by southern notoungulates and advanced arctostylopidids would have been acquired independently and therefore represent parallelisms. These include the reduction of the lower molar trigonids, the addition of accessory trigonid structures to those teeth (the homology of these structures, termed pre- and postmetastylid by Marshall, de Muizon, and Sigé, 1983, is open to some question, even among the taxa restricted to South America), the development of a talonid on P₄, and the upper molar crown pattern, which is superficially similar but appears on other grounds to include non-homologous features, as discussed above. What is known of the ankle region in arctostylopidids indicates that they are divergently specialized from notoungulates. One specialization of the arctostylopid ankle, the development of the calcaneal fibular facet into a large, semicylindrical surface, is found among a group of advanced toxodont Notoungulata (the monophyletic group including Notohippidae, Leontiniidae, and Toxodontidae), but this was clearly developed independently by them. Certain other notoungulate resemblances of arctostylopidids, which undoubtedly influenced early workers in their comparisons and in their speculation regarding relationships, evidently represent derived character states within *both* groups and are almost certainly convergent. These include the presence of a labial ectocingulid, which is characteristic of most toxodont lower molars and premolars and of advanced forms (e.g., *Palaeostylops*, *Gashatostylops*, and *Arctostylops*) among the Arctostylopidae. The smooth ectoloph of advanced arctostylopid upper molars

(*Anatolestylops*; unnamed genus and species), which lacks folds other than those for the parastyle and metastyle, is reminiscent of that of notoungulates such as *Notostylops* (comparison with which was the basis for the genus and family-group names of the northern forms) and various Leontiniidae, but primitive members of both the Arctostylopidae and southern Notoungulata have lower, more complexly folded ectolophs. *Arctostylops* and ?*Palaeostylops* also resemble some southern notoungulates, especially *Notostylops*, in the high talonid crescent, which achieves an anterior attachment with the trigonid at a very labial position; this, again, is not a condition shared by more primitive members of either group.

Remaining Resemblances

With the dismissal of many arctostylopid-notoungulate similarities as convergent acquisitions within each group, it is relevant to evaluate the uniqueness of resemblances that remain. The most striking of these is the transversely developed, lophate entoconid (entolophid) of the lower molars. This is an unusual but not exceptional feature among mammals: it surely developed independently in the Astratheria and twice among the Litopterna (Cifelli, 1983a; Cifelli and Soria, 1983). Among Holarctic mammals, an entolophid or similar structure developed independently in numerous rodent lineages (L. L. Jacobs, personal communication). Without knowledge of more primitive forms, it is not possible to determine if the arctostylopid entolophid arose, as in the southern notoungulates, from part of the posteristid or if it is demonstrably non-homologous (the entolophid of astratheres, for instance, appears to be a *de novo* structure). If, as argued by Marshall, de Muizon, and Sigé (1983), *Perutherium* is a notoungulate, then independent acquisition of the entolophid in the Arctostylopidae is suggested by the fact that they primitively lack the accessory trigonid structures possibly shared by that genus with Neotrop-

ical Notoungulata. Other shared dental features of arctostyloids and notoungulates, derived with respect to an ungulate morphotype, might include a crescentic lower molar trigonid (this condition is somewhat uncertain in southern notoungulates, as the trigonid is already reduced at first appearance), reduced upper molar styler shelf and lobes, and slightly raised centrocrista between paracone and metacone on the upper molars ("incipient" ectoloph). These latter features are not in themselves or collectively diagnostic, as they represent generalized, almost gradal trends in many different groups of Paleocene and Eocene ungulate-like mammals.

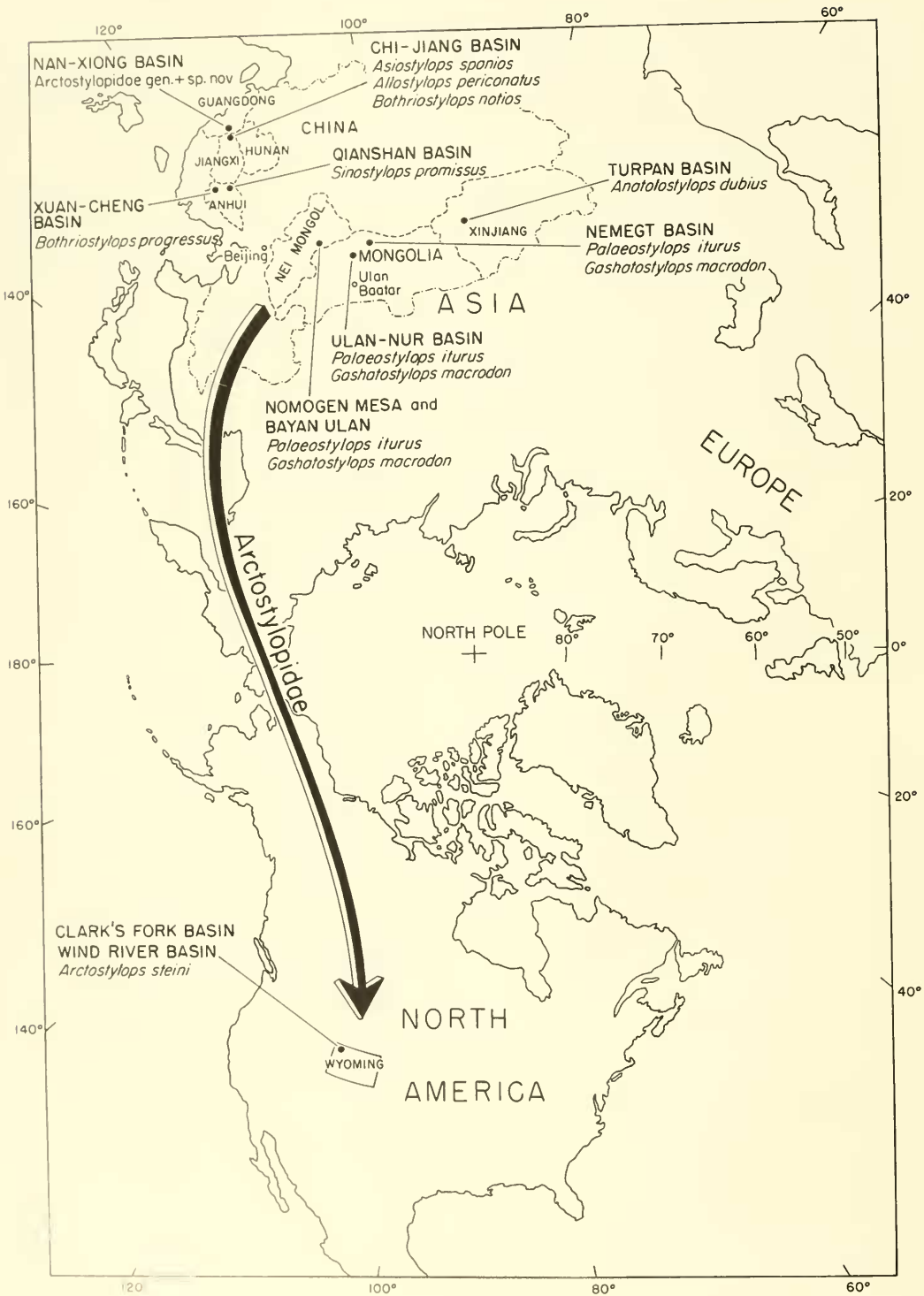
Of the three alternatives of arctostyloid-notoungulate relationships discussed above, the most permissive, that they represent sister taxa, is the most likely. (This is true by definition, as the other two possibilities are more specific and therefore more susceptible to falsification.) Yet, because most similarities of arctostyloids to notoungulates must have arisen independently, whether by parallelism or convergence, the evidence that they collectively comprise a monophyletic unit with respect to other mammals is slim: it amounts, in fact, to one possible character (entolophid) that is known to have developed independently several times among other, unrelated groups. This is hardly secure documentation of monophyly. Other evidence, such as that provided by the ankle region, suggests that a common ancestor of the two groups would have been exceedingly primitive and, probably, not exclusive.

Distinctness of Arctostylopida

Since the time of Ameghino, many close relationships of South American with Holarctic forms have been proposed (see, e.g., summaries by Simpson, 1978; McKenna, 1981; and Gingerich, 1985). With the exception of marsupials, the controversy surrounding all ordinal and lower level referrals of South American to Holarctic taxa has been considerable, in part because derived similarities are incomplete or not un-

ambiguously homologous, and in part because the evidence of relationship has often been based on shared primitive features rather than uniquely derived specializations. The Arctostylopidae have been immune to such controversy because, despite some unique aberrancies and retention of a few primitive features, the advanced genera *Arctostylops* and *Palaeostylops* strikingly resemble notoungulates and no other mammals in certain aspects of their dental anatomy. Evaluation of the reality of this relationship and its precise nature was long hampered by insufficient knowledge of arctostyloid morphologic diversity and of the structure and relationships of the most primitive notoungulates of South America. With these circumstances now dramatically improved, considerable doubt is cast on the close relationship of the two groups, accepted without question for most of this century. A common notoungulate/arctostyloid ancestor (i.e., a morphotype for the two groups, considered as sister taxa) might have been sufficiently primitive to have given rise to many other orders of mammals. In recognition of this, and considering the ample evidence for monophyly of the Arctostylopidae, we have referred the family to its own order. Thus recognized, the group would represent an Asian radiation that managed to disperse to North America, possibly in the late Paleocene. The geographic distribution of arctostyloid taxa, and the hypothesized immigration to North America, are given in Figure 13. It is interesting to note that most of the primitive forms are more southerly in distribution, being found in south China, while specialized taxa are generally northerly in distribution.

The broader relationships of Arctostylopida among the Mammalia are enigmatic. The arctostyloid dental morphotype bears some similarity to several Asian taxa of debatable affinities, such as *Lantianius* (Cifelli, 1983a) and *Petrolemur*, although contrasting specializations (such as loss of premolars in the latter genus) are



evident. Both forms were originally referred to the Primates; the ankle of known arctostyloids is completely dissimilar to any belonging to that order. Arctostyloid ankle specializations are shared, as best we are able to determine from published figures (Sulimski, 1968; Szalay, 1977, fig. 16), with the Asian late Paleocene *Pseudictops*. This taxon has, in turn, been considered to be part of "an endemic Cretaceous and early Tertiary Asian radiation, whose closest living relatives are the Lagomorpha" (Szalay and McKenna, 1971, p. 301). Whatever the constituents of this radiation (see also McKenna, 1975; Novacek, 1986; Szalay, 1977), we note that lagomorphs and some of their suspected allies are specialized for saltatory locomotion (Szalay, 1977; see Bleefeld and McKenna, 1985, for description of some lagomorph ankle specializations); arctostyloids—which may just be primitive in this regard—apparently were not, as indicated by the lever mechanics of the calcaneus.

The diversity and abundance of arctostyloids in early Tertiary Asian faunas, coupled with the proposed close relationship of North American *Arctostylops* to Asian *Palaeostylops* as rather derived taxa within the family, suggests that dispersal from west to east, rather than the reverse, is the most probable explanation for geographic distribution of the group. Owing to high endemism of Asian faunas older than those of the North American Wasatchian, correlation of earliest Tertiary mammalian assemblages between the two continents has been problematic (Szalay and McKenna, 1971). The presence of *Arctostylops* in the Tiffanian (late Paleocene) of North America, the geometry of proposed relationships among the Arctostylopidae, and the fact that more primitive taxa are known from Asia but not North America, suggest a late Paleocene (Dashzeveg, 1982; Szalay and McKenna, 1971),

rather than early Eocene (Gingerich and Rose, 1977) age for Asian faunas, such as Gashato, which include *Palaeostylops* and *Gashatostylops*.

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Figure 13. Lambert's azimuthal equal area projection map of Northern Hemisphere, showing arctostyloid distribution and hypothesized dispersal route to North America.

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